"Anything that can be said verbally can be said better non-verbally."

Irving A. Taylor. Ph. D.

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THE INTERTIDAL ECOLOGY OF THE ROCKY SHORES OF THE KAIKOURA PENINSULA

A thesis presented for the
degree of Doctor of Philosophy in Zoology
in the University of Canterbury,
Christchurch, New Zealand.

by

Robert A. Rasmussen

1965

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A LIST OF ILLUSTRATIONS

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Plates

An Ecological Survey of the Intertidal Rocks of the Kaikoura Peninsula.

Introduction

In recent decades, considerable attention has been focused on the biology of intertidal regions.

Although a major impetus to intertidal studies was, undoubtedly, the work of T.A. and Anne Stephenson in South Africa (Stephenson, T.A. 1939, 1944, 1947) (Stephenson, T.A. and Anne Stephenson. 1949), the bulk of the subsequent work has been done in the Northern Hemisphere. To date, the majority of Southern Hemisphere studies have been descriptive field studies.

The Southern Hemisphere works have recently been reviewed and bibliographied by G.A. Knox (Knox, in Barnes. 1963). As a more general bibliography of shore studies, as well as of taxonomic and autecological studies, the annotated bibliography by Joel Hedgpeth, in "Between Pacific Tides" (Hedgpeth in Ricketts, E. and J. Calvin 1962) is recommended.

G.A. Knox (1953) stated that a series of studies of the rocky shores of the South Island of New Zealand have been under way since 1948. This paper is meant to be a contribution to that series.

The Kaikoura Peninsula is one of a series of large peninsulas on the east coast of South Island. The Otago Peninsula and the Banks Peninsula to the south have been surveyed, at least in part, (Batham 1956, 1958) (Knox 1953) making the Kaikoura Peninsula "next in line", as it were. Further, the Kaikoura Peninsula is at a point corresponding

to certain distributional limits of shore species and marks the northern position of the Sub-tropical Convergence, a meeting of sub-tropical and sub-antarctic currents. These factors, plus the final and decisive factor of accessibility to the railway and highway and the borough of Kaikoura contributed to the locating of the Edward Percival Marine Laboratory of the Zoology Department of the University of Canterbury on the Kaikoura Peninsula.

This survey is the result of over two years continuous residence in Kaikoura as a full-time research student at the Edward Percival Marine Laboratory.

The Environment

The Geography and Geology of the Kaikoura Peninsula.

i. The Kaikoura Peninsula is located between 42°25'11" and 42°23'22" South latitudes and between 173°39'00" and 173°44'00" East longitudes, on the eastern coast of the South Island of New Zealand. It projects approximately two and one-half miles out from the Marlborough Coast.

ii. The peninsula may be conveniently divided into two parts: a base, and the peninsula proper. The base, or isthmus, of the peninsula is about one mile long and is just under three-quarters mile wide at its narrowest point, where it joins the peninsula proper. The shores of the base, like the shores of the adjoining coast, are mainly exposed shingle beach.

The peninsula proper is, roughly, an equilateral paralellogram, one and one-half miles to the side, and bearing various bays and points. This shape results in three distinct and complete faces of the peninsula being exposed to the sea. The fourth side is mainly the connection with the peninsula base (Fig. 1).

The peninsula proper is a hilly plateau with an average elevation of more than three hundred feet. At each seaward face, the land drops sharply to a narrow shelf that slopes gradually into the sea. The shelf then terminates within the intertidal region by dropping sharply to the sea floor.

Of the approximately one and seven-tenths square miles (4.4 sq. km.) of the peninsula proper, the intertidal shelf represents slightly more than three-tenths square miles (.77 sq. km.).

iii. Two synclines and the intermediate anticline, at right angles to the long axis of the peninsula, have formed an alternation of limestone and siltstone platforms along the northeast and southwest faces of the peninsula (Fig. 1). The limestone surfaces, generally rough and broken due to the repeated folding of the limestone layers, form steep ridges throughout the intertidal range (Pls. 7 & 18). The softer siltstone shows no obvious signs of layering. Constant erosion has levelled the platforms, corners and sharp edges are exceptional (Pls. 9 & 16). The siltstone platforms are generally broad, smooth, gently sloping towards the sea then rising slightly at the seaward edge to give a parapet effect. (Fig. 7).

Figure 1 and Table 1, compiled from information provided by the New Zealand Geological Survey (N.Z. Geo. Survey, Sheet 16, 1963), summarize the intertidal substrates of the peninsula.

Table No. 1

Summary of intertidal substrata - Kaikoura Peninsula

Corresponding Platforms		Substratum	Topography
Northeast Face	Southwest Face		
Laboratory Rocks	Moa Point	Nodular flinty limestone overlain by Amuri limestone	Max. platform width, 3ch (60.5m) Steeply sloping surfaces
Avoca Point	Limestone	Amuri limestone	" "
Armer's Beach Wairepo Flats	Mudstone Bay Flats	Glauconitic siltstone	Avg. platform width, 5ch. (100.6m)
Lighthouse Point (Kean's Pt.)	Sharkstooth Point	Argillaceous siltstone	Slopes of 1:50-1:100 Edges nearly vertical
Southeast Face			
Second Point Sugarloaf Point Fourth Point		Amuri limestone mixed with Weka Pass stone bands	Highly contorted
Exposed tips of First Point Second Point and Sugarloaf Point		Argillaceous siltstone	Smooth surfaces curving into the sub-littoral

Climate

The Kaikoura Peninsula is in the South Temperate Zone. The winters are mild along the coastal plain. Frosts occur sporadically from June through September. These frosts occur at night and are dissipated by the morning sun. Freezing temperatures are rare along the open coast and a twenty-four hour frost would be most exceptional. Snow and frosts are common within a very few miles of the shores but along the coast the temperatures are tempered by the warmer ocean mass.

Summers are warm. However, hot spells are infrequent and of short duration. This, also, can be credited to the tempering effect of the ocean mass. Summarized air and sea temperatures are given on Fig. 2. Air temperatures were recorded at the Kaikoura station of the N.Z. Meteorological Service. This station is located on top of the peninsula, approximately three hundred feet above the shore. Sea temperatures were recorded at the New Wharf on a continuously recording thermometer.

Winds are predominately from the South and Southwest in the winter and from the Northeast in the summer (Fig. 3). Rarely, a strong, dry, northwesterly wind occurs, doing much damage to vegetation. The last such wind was recorded in 1959.

Rainfall and sunshine data for 1962-1965 are summarized on Figure 5. The expected trend of increased sunshine with the increase of day length is evident. Seasonal patterns in rainfall are not particularly evident from these records though the local residents feel that July and August tend to be "wet months" and expect a "dry spell" around October or November.

Hydrology - Off Shore

i. Three miles to the east of the Kaikoura Peninsula the continental shelf gives way to the continental slope, which descends sharply from forty three fathoms to two hundred forty nine fathoms (Admiralty 1953). The sea floor then slopes more gently to the bottom of the southern extremity of the Hikurangi Trough of the Kermadec Trench. A depth of 1500 fathoms is reached at a point approximately twenty-one miles southeast of the peninsula.

Similarly, the Kaikoura Trench lies parallel to the coast just south of the peninsula (Admiralty 1953b).

ii. A comparison of water temperatures given by Garner (1961) and the temperatures recorded at the New Wharf show that the temperature range for the intertidal waters and the waters over the shelf are the same. Recent comparisons made with readings taken off-shore show less than 0.5^{o}C. variation at any given time (J. Grieve, pers comm.). The annual temperature range of the intertidal waters is 9.5 Centigrade degrees, from 8.5^{o}C. to 18.0^{o}C. (Fig. 2).

Salinity studies (Houtman, in Press) indicate that there is a constant light dilution of in-shore surface waters. This coincides nicely with salinity patterns published by Garner (1961). Garner indicates a salinity range of $34.3^{o}/00$ to $34.6^{o}/00$ for the waters just off-shore of the peninsula. A series of salinity determinations were made of the intertidal waters at Ingles Bay and South Bay (Table 2). Values ranged from $32.9^{o}/00$ to $35.0^{o}/00$. These values indicate that the in-shore waters have approximately the same salinities as the off-shore waters but that they often, though not always, show dilution.

There are no rivers, or sizeable streams, on the peninsula. However, there are rivers and streams short distances to the North and the South of the peninsula. It would seem that most of the dilution is from seepage, and run-off after rains, as dilution due to the neighbouring rivers would be more constant.

iii. Drift card experiments by Brodie (1960) and the temperature and salinity measurements of Garner (1959, 1961) indicate that the Kaikoura Coast occasionally receives an influx of sub-antarctic water from the north flowing North Canterbury Current that is just off-shore of the southern east coast of the island. Generally, the waters are derived from the sub-tropical East Cape Current which comes down from the north.

Table No. 2

Salinity determinations (modified Mohr method) °/00

Date	Ingles Bay	South Bay
30 Aug 63	34.2	--
16 Sep 63	32.9	33.7
30 Sep 63	33.3	34.0
18 Oct 63	34.0	34.2
15 Nov 63	34.1	34.6
19 Dec 63	34.8	35.0
26 Jan 64	34.8	--
5 Mar 64	33.9	34.2

A general account of the course of these currents and their meeting as the Subtropical Convergence is given by Knox (1960).

The evidence of the corresponding temperatures, similar salinities, and the narrowness of the shelf indicates that the intertidal waters of the Kaikoura Peninsula are open ocean waters rather than coastal waters.

Hydrology-Tides

i. The tides are semi-diurnal. There is a slight difference in the range of the day and night tides. The maximum predicted difference for any twenty four hour period during 1962-1964 was 0.6 feet. Differences of 0.1 to 0.2 are the rule. The maximum predicted range of a spring tide is 6.7 feet. The minimum predicted range for a neap tide is 2.7 feet.

Spring tides occur, on the average, every twenty eight days. However, this period is not quite constant. During the year, the spring tides narrow their range while the neap tides widen their range until there is a long period of indeterminate tides and then the tides that were the springs become the neaps and the neaps become the springs. This change occurs twice in every twelve to fourteen months (Admiralty 1962, 1963, 1964).

ii. Records now available from a continuously recording tide gauge on the New Wharf indicate that the predicted figures vary considerably from the actual levels. Times of high and low water may vary as much as one hour from predicted times. The tidal levels often vary considerably from the predicted levels. These variations can usually be correlated with weather conditions.

The tidal crest follows the east coast of New Zealand from the South to the North. The prevailing winds, in this area, also follow the coast - in either direction. The peninsula lies at right angle to the path of both the tidal crest and the prevailing winds. Southerly winds tend to hasten the arrival of the tidal crest causing the tide to be

early and to be higher on the southwest face and lower on the northeast face. Conversely, northerly winds tend to delay the arrival of the crest causing the tides to be late and causing the highs to be low and the lows on the southwest face to be lower and the lows on the northeast face to be high.

A graphic example of wind effect on the tidal levels came to hand on September 27th, 1963. Measurements of the water level were being taken on the southwest coast of the peninsula in an effort to determine the relative levels of some bench marks. During the morning, while the tide was in, the wind was from the South at less than ten knots. Between Noon and 1300 hours, the wind switched to the Northeast, building up to twenty knots staying in that quarter until long past low water. The predicted tidal range for that day was 3.2 feet. The actual range was measured at 4.35 feet. The tidal measurements and wind conditions are summarized on Fig. 6.

These variances indicate that the predicted levels of the tide do not suffice for analysis of biological phenomena on the shores and that any exposure indices, critical levels, etc. based only upon predicted levels are suspect.

Hydrology - Wave action

i. Four major factors appear to determine the degree of wave action on the shores of the peninsula. Three are, to some extent, measureable. They are wind direction, wind velocity, and bottom configuration. The fourth factor, a compound factor, is non-local weather conditions. This factor, or combination of factors, superimposes its effect upon the effects of the other three factors in such a way that it always increases the violence of the wave action. A study of the measureable factors makes it possible to predict the minimal wave action of a given local weather pattern but the fourth factor makes further analysis impossible, at present.

ii. Observations were made throughout the year, at such times as it was judged that non-local conditions were minimal. It was noted that all winds having a southerly bearing, i.e., Southeast, South, Southwest, had similar effects. The same was true of winds with northerly bearings. It was also noted that the effects of wind velocity could be divided into two categories: effects of winds less than ten knots, and effects of winds over ten knots. Finally, because of the nature of the intertidal shelving, it was found necessary to compare wave actions at "low tide" (ELWS-ELWN), "mid tide" (ELWN-EHWN), and "high tide" (EHWN-EHWS). Thus, thirteen situations were established for observation:

Strong, northerly winds at low tide, mid tide, and high tide
Gentle, " " " " " " "
Strong, southerly winds " " " " "
Gentle, " " " " " " "
and, Calm, at all levels.

Subjectively, wave action was divided into six categories:

O - Glassy smooth, little or no swell.

I - Ripples, very gentle swells, enough to effect the wetting of organisms no more than 0.2 feet (6cm.) above the absolute tide level (Pl. 1).

II - Waves with repetitive patterns and/or gentle swells strong enough to carry water several inches up vertical faces, without breaking (Pl. 2).

III - Waves that break on vertical, and near vertical, surfaces, or that crest and break over shallows (Pl. 3).

IV - Waves that break, throwing horizontal spray upon meeting resistance. These waves have a considerable pounding and wetting effect well above the tide level (Pl. 4).

V - Waves that throw spray vertically upon meeting resistance, causing a maximum pounding effect (Pl. 5).

As a result of the observations made (Appendix 1), it was possible to define four types of shoreline (Fig. 4). An outer surf belt (A) surrounds the peninsula. Rocks and reefs in this area are subject to class IV waves under gentle winds and to class V waves under strong winds. Wind direction is not important in this area. Nearly all of the rocks and reefs in this surf belt have steep faces that extend well below the low water line. Therefore, quite high waves develop, sending water over the tops of the rocks. These rocks are seldom dry. Only during exceptionally long calm spells do the waves, or swells, drop to class III.

The area (B) just within the surf zone, is affected more strongly by the wind direction.

In this area, strong on-shore winds can cause class V waves, particularly at low tide when numerous steep rock faces are exposed. Class IV waves are the predominant feature of this region occuring during both strong off-shore winds and gentle on-shore winds. Gentle off-shore winds generally produce class III waves.

The southeast face is parallel to the prevailing winds. All winds can be considered on-shore winds for this face.

The area (C) interior to the areas of heavy wave action represents shallow water and areas reached only at high tide. The depth of water will only support class III waves. Strong off-shore winds and gentle on-shore winds produce class II waves and gentle off-shore winds produce class I waves.

Sheltered areas (D) are very shallow, Class II waves are the largest that can be generated by strong on-shore winds. Other wind conditions produce only class I or class 0 waves.

Table No. 3

Summary of wind-wave relationships

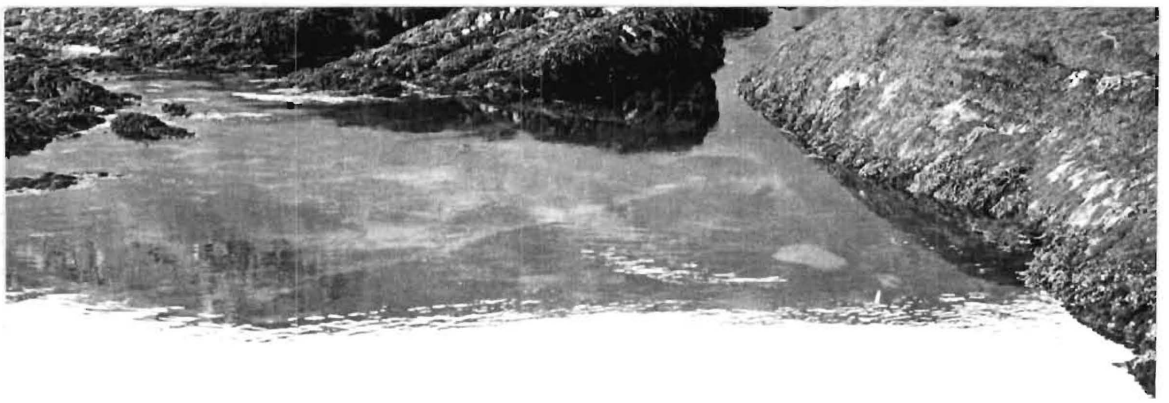
Wind	on-shore		off-shore		
Strength	strong	gentle	strong	gentle	calm
Area					
A	V	IV	V	IV	III
B	V	IV	IV	III	II
C	III	II	II	I	I-0
D	II	I	I	0	0

Plate 1.

Class I wave action (wind ripples) at Wairepo Flats in a (D) zone. (Photograph R.A. Rasmussen, 11 June 1964.)

Plate 2.

Class II wave action as seen from the New Wharf, facing across to Wakatu Point through (C) and (B) zones. This picture was taken on 30 April 1965, after a southerly front had passed. It was taken only a few minutes after the Class IV & V pictures (Pls. 4, 5). This is a good demonstration of the effect of wind direction. (Photograph J.T. Darby).



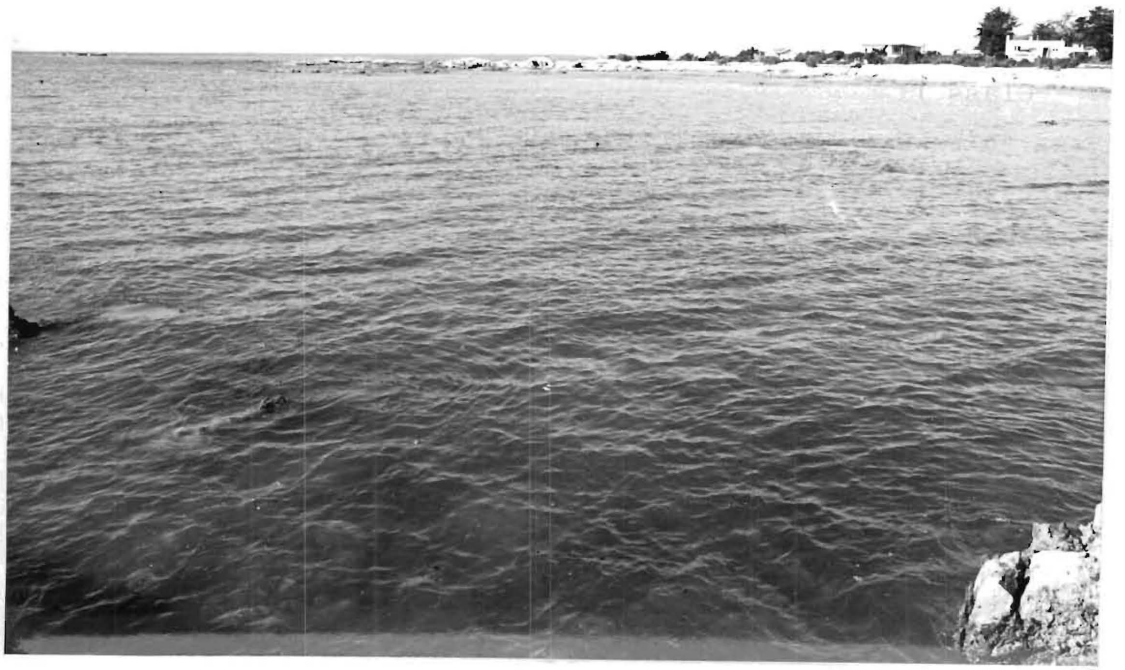


Plate 3.

Class III wave action at Avoca Point in a (C) zone during strong on-shore winds. Calmer water is apparent in the background at the entrance to Armer's Beach, a (D) zone. (Photograph R.A. Rasmussen, 15 March 1965.)

Plate 4.

Class IV wave action breaking over rocks in the (B) zone on the western edge of Sharkstooth Point. Taken just after a southerly front had passed. (Photograph J.T. Darby, 30 April, 1965.)

Plate 5.

Class V wave action at the tip of Sharkstooth Point. (Photograph J.T. Darby, 30 April 1965).

The Organisms

Survey techniques

i. The Kaikoura shores were under nearly daily observation during 1963 and 1964. They were also visited fortnightly during the first six months of 1965. Early in 1963, twelve sites were chosen for detailed observation. These sites were chosen to represent large areas of fairly uniform animal and plant distributions. Bench marks, consisting of large carriage bolts set in concrete, were placed on, or near, each site. Bench mark locations are as follows:

1. Near the high water mark, on a limestone out-cropping, in front of the Edward Percival Marine Lab.

2. On a concrete retaining wall between the Pier Hotel and the New Wharf.

3. Near the high water mark, on the limestone platform, at the tip of Avoca Point.

4. Near the high water mark, on the siltstone platform, near the tip of Avoca Point, very near number 3.

5. 6 & 7. In a triangle, on the siltstone of Seal Reef, about one hundred meters to the Northeast of the limestone formation that supports the Red-billed Gull rookery.

8. At the base of the cliff on Lighthouse Point, about one hundred meters from First Bay.

9. On a high point, mid-way out the eastern edge of the Sharkstooth Point platform.

10. Near the high water mark on the Mudstone Bay platform.

11. Above the high water mark, on a limestone out-cropping, at the tip of Waeroa Point.

Another reference point was determined, but not marked.

with a bench-mark, at the base of the Automobile Association sign "Watch for Stock", on the roadway in front of the Symes homestead at Wairepo Flats.

The relative levels of these points were determined by measuring tidal curves at each location. Observations were made alternately at two sites, throughout the same day, and the curves were plotted on the same graph. By choosing calm days, and going rapidly from point to point, it was possible to obtain curves that could be related to the curves obtained from the recording tide gauge on New Wharf. All the levels were then related to the Zero on the tide staff on the New Wharf. Several repetitions of the measurements were made and an error of less than 0.1 foot is indicated.

The bench marks were then used to determine the profiles of twelve transects (Fig. 7), and to relate them to the tidal levels obtained from the tide gauge. All measurements of relative levels: of water levels, of rock levels, and later of the vertical position of organisms, were made by sighting across two vertical, calibrated poles to the ocean horizon. A similar method has been described by Morgans (1957), and by others. The unit of measure chosen was tenths of a foot as this is the unit used in the Admiralty Tide Tables and is as small a unit as practical.

Each transect was one meter in width. Notes were made of the levels and abundance of each species present and observations were made of the surrounding areas to ensure that the condition of the transect was representative.

Concentrations of sessile animals and plants on the transects were estimated in terms of per-cent cover.

Mobile organisms were counted with counting frames. All estimates and counts were then scaled into six abundance classes and the results are represented graphically on Figures 8 through 19. Table 4 indicates the numerical range of each abundance class for each organism.

Transects were visited at almost every spring tide, during the period of January 1963 through June 1964. Four or five transects were observed during each week of spring tides so that each transect was visited once in every three months, at the very least. Other visits were made to the transects at irregular intervals, as the mood moved or the need for specific information occurred.

ii. Further notes were made during frequent but irregular walks about the coastline. These notes consist of descriptions of community patterns, habits of species with limited distributions, reproductive cycles, and seasonal changes. These notes were kept in diary form.

Table No. 4

Abundance scales used for comparison of transects

1. Plants and sessile animals

Abundant	85 - 100% of total cover
	65 - 85%
	45 - 65%
	25 - 45%
	5 - 25%
Present	less than 5%

2. Melaraphe spp.

Abundant	over 4500/m^2
	3500 - 4500/m^2
	2500 - 3500/m^2
	1500 - 2500/m^2
	500 - 1500/m^2
Present	less than 500/m^2

3. Melagraphia aethiops

Abundant	over 125/m^2
	100 - 125/m^2
	75 - 100/m^2
	50 - 75/m^2
	25 - 50/m^2
Present	less than 25/m^2

4. Lunella smaragda

Abundant	over 80/m^2
	60 - 80/m^2
	40 - 60/m^2
	20 - 40/m^2
	1 - 20/m^2
Present	less than 1/m^2

5. Cellana spp.

Abundant.....over 160/m^2

.....120 - 160/m^2

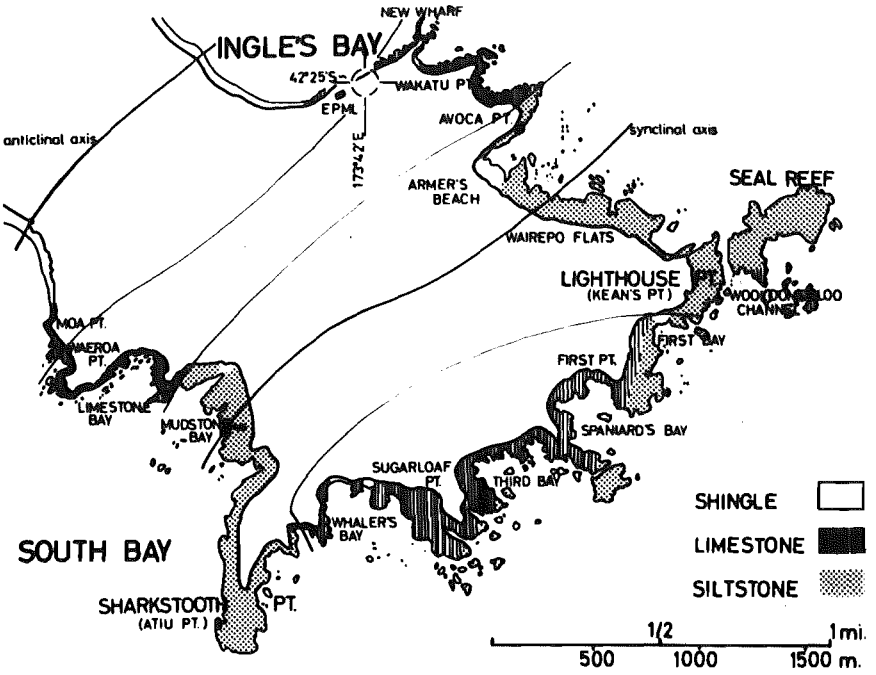
..... 80 - 120/m^2

..... 40 - 80/m^2

..... 1 - 40/m^2

Present ..... less than 1/m^2

6. Other species occurred only in the Present category, or had such irregular distributions that it was difficult to ascribe an abundance maximum to them.


INGLE'S BAY
NEW WHARF
42°25'S
WAKATU PT
EPML
173°42'E
AVOCA PT
anticlinal axis
synclinal axis
ARMER'S BEACH
SEAL REEF
WAIREPO FLATS
LIGHTHOUSE (KEAN'S PT)
WOOLOOMOOLOO CHANNEL
MOA PT
WAEROA PT
FIRST BAY
FIRST PT
LIMESTONE BAY
MUDSTON BAY
SPANIARD'S BAY
SUGARLOAF PT
THIRD BAY
WHALER'S BAY
SOUTH BAY
SHARKSTOOTH (ATIU PT.) PT
SHINGLE
LIMESTONE
SILTSTONE
1/2
1 mi.
500
1000
1500 m.

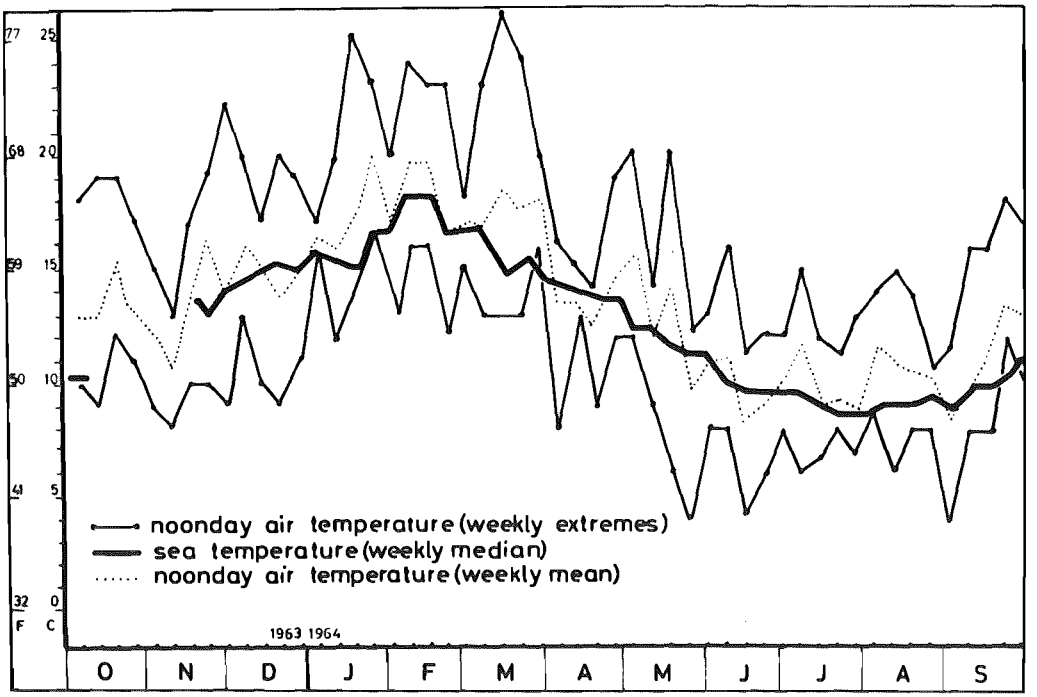

77 25
68 20
59 15
50 10
41 5
32 0
F C
noonday air temperature (weekly extremes)
sea temperature (weekly median)
noonday air temperature (weekly mean)
1963 1964
O N D J F M A M J J A S

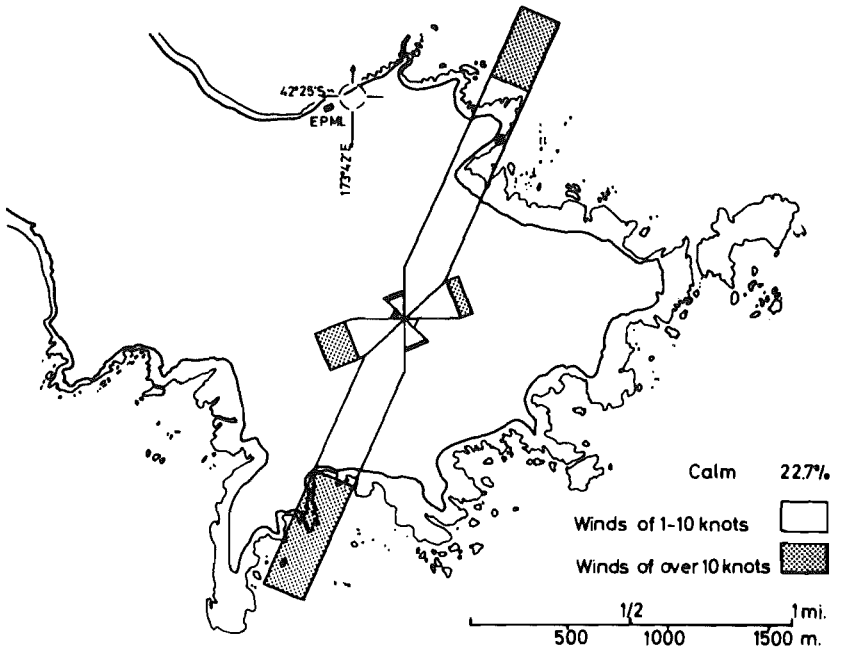
Figure 1.

A map of the Kaikoura Peninsula, drawn from aerial photographs supplied by the Department of Lands and Survey, showing the place names used in this paper.

The geological information was obtained from field maps of the peninsula provided by the New Zealand Geological Survey.

Figure 2.

Air and sea temperatures for one year. Air temperatures were recorded daily at 0900, 1200, and 1500 by the Kaikoura station of the New Zealand Meteorological Service. Sea temperatures were averaged weekly from the records of the continuously recording thermometer installed on New Wharf.


42°25'S
EPML
173°42'E
Calm 22.7%
Winds of 1-10 knots
Winds of over 10 knots
1/2
1 mi.
500
1000
1500 m.

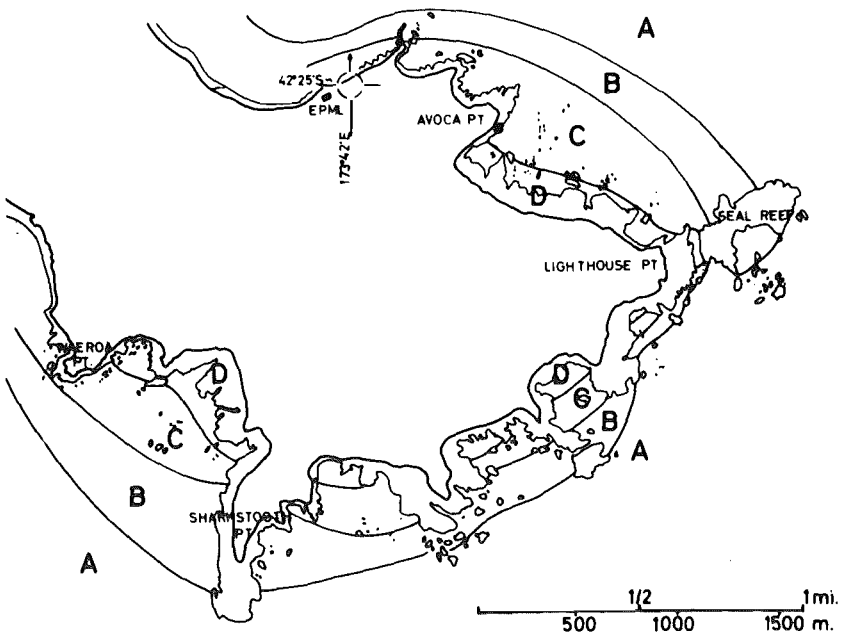

A
B
C
D
42°25'S
EPML
173°42'E
AVOCA PT
SEAL REEF
LIGHTHOUSE PT
SHAMROCK PT
1/2
1 mi.
500
1000
1500 m.

Figure 3.

A wind rose for the Kaikoura Peninsula based upon hourly observations from 0800 to 1600 hours, during one year (September 1963-August 1964). Information supplied by the Kaikoura station of the New Zealand Meteorological Service.

Figure 4.

A map summarizing the wave action around the Kaikoura Peninsula, cf. pp. 14, 15 for definition of zones A-D and Appendix 1 for detailed data maps.

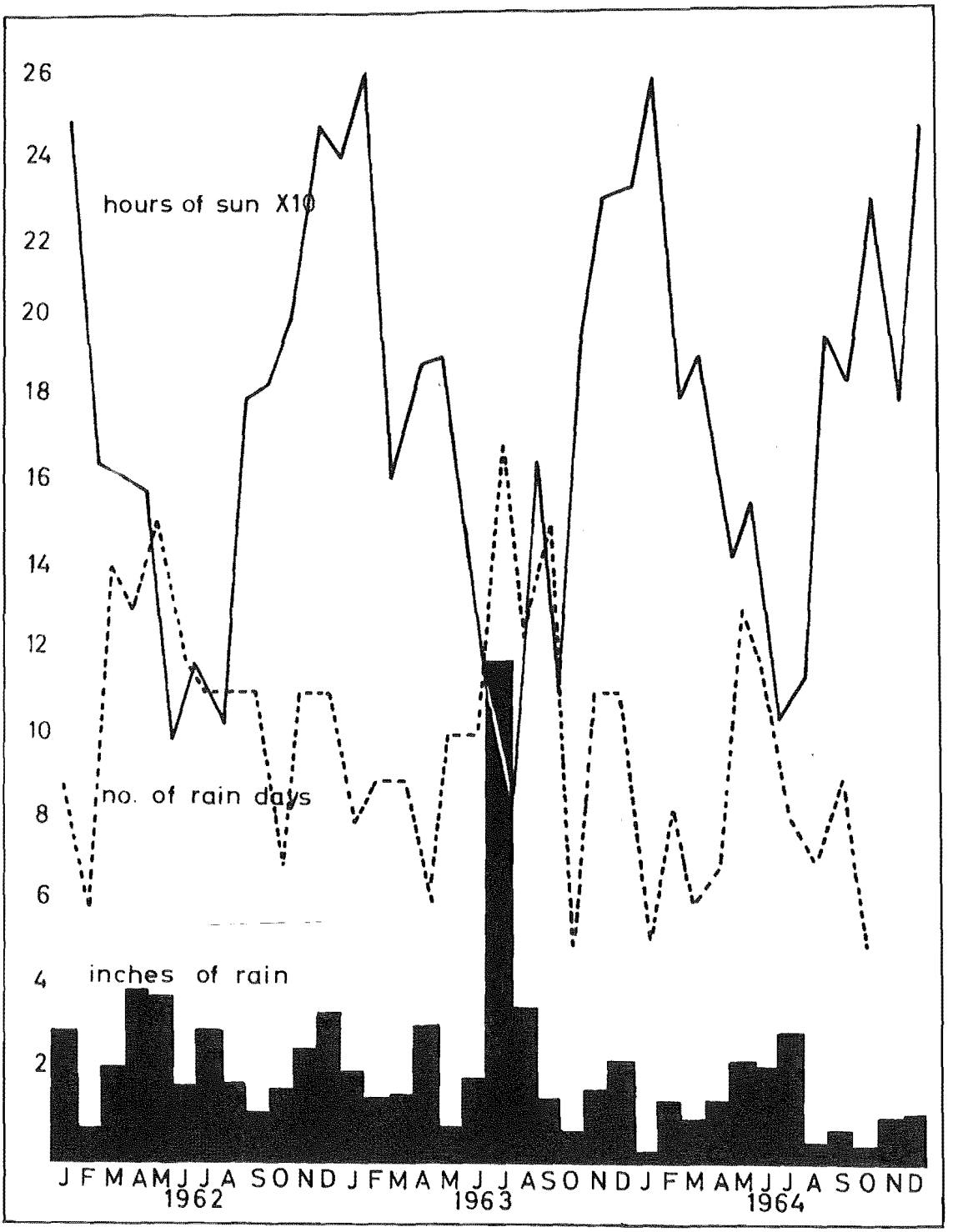
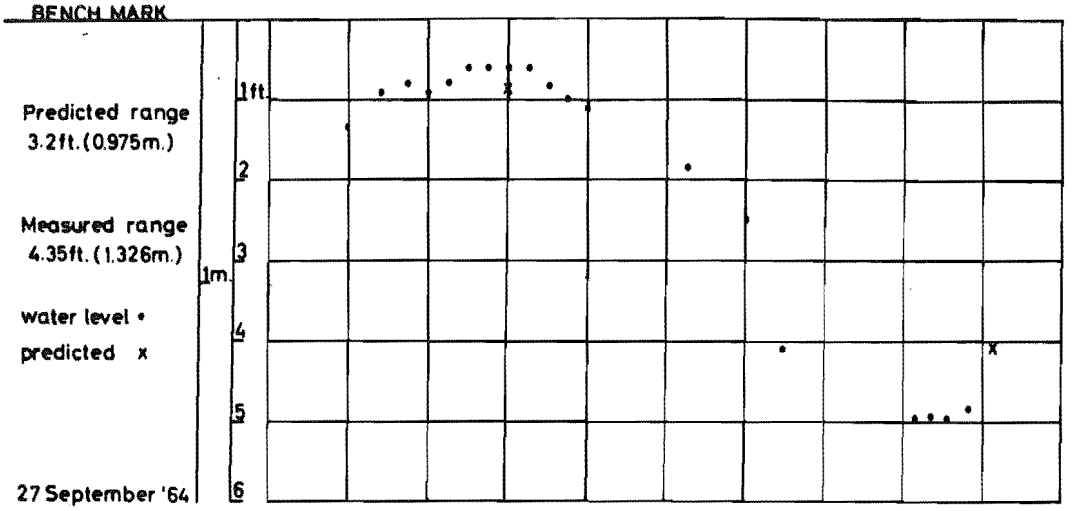

26
24
22
20
18
16
14
12
10
8
6
4
2
hours of sun X10
no. of rain days
inches of rain
J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D
1962
1963
1964

Figure 5.

A summary of sunshine and rainfall data for 1962-1964 supplied by the Kaikoura station of the New Zealand Meteorological Service.

The sunlight hours were recorded by a burning glass and represent only "direct" sunlight. The rainfall data was collected from daily readings of a standard rainfall gauge.

BENCH MARK



TIME	0900	1000	1100	1200	1300	1400	1500	1600	1700	1800	1900
WIND DIRECTION	190	180	180	170	080	060	060	040			
WIND SPEED(KNOTS)	10	07	05	03	03	05	09	09			

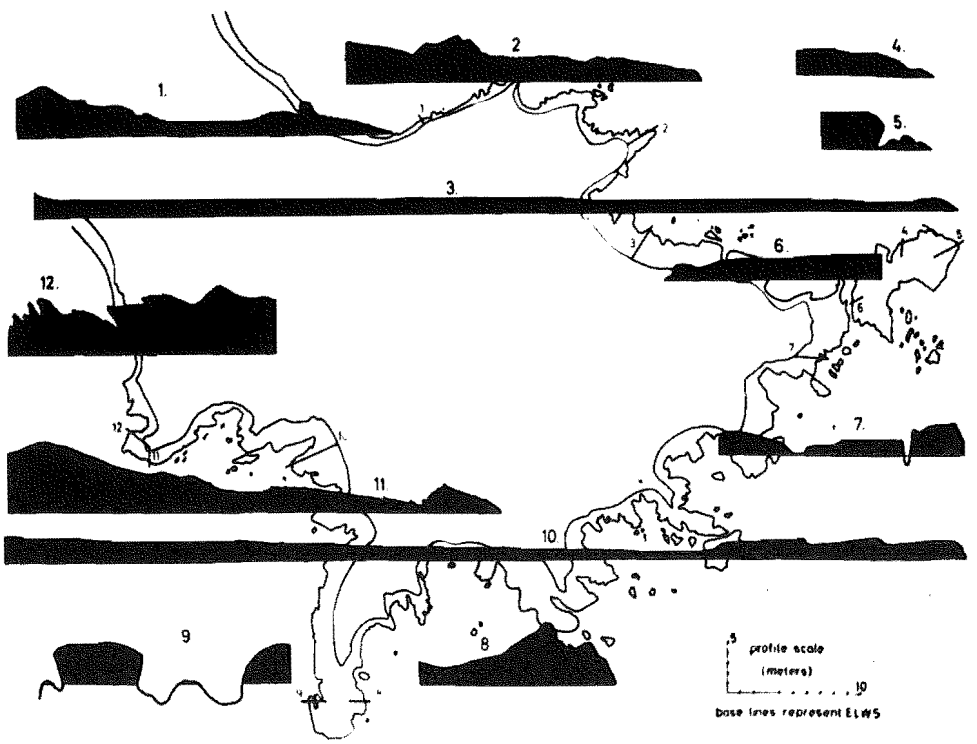


Figure 6.

The tidal curve for 27 September, 1963 taken at the Mudstone Bay Flats. The effect of wind direction and velocity can be seen by comparing the predicted high and low levels (X) with the actual levels recorded. The tide range was extended 35.9% on this occasion.

Figure 7.

A map showing the location and profiles of the twelve transects studied in detail. Numbers 1, 2, 11, and 12 are on limestone platforms. The remainder, numbers 3-10, cross siltstone platforms.

Terminology

i. A universal, or nearly universal, feature of the intertidal region is the distribution of the organisms into horizontal bands. These bands may be obvious and discrete as in the case of organisms with a high concentration and both vertical limits within the tide marks, or they may be indistinct, in the case of organisms with a low concentration and/or only the upper limit in the intertidal. Recognition of the similarities in the patterns of distribution on different shores has led many authors to devise systems of nomenclature that would allow a comparison to be made with any shore. All of these systems have been found wanting in one particular or another. The most successful scheme, among those used by English speaking writers, has been that of the Stephensons (1949, 1953). However, this scheme has also had its critics. Recently, J.R. Lewis (1961, 1964) has proposed a modification of the Stephenson scheme that is reasonable, easily applied, and requires very little change in usages now current. This system divides the world near the sea, and in the sea, into three areas.

That area inhabited by terrestrial organisms, or organisms with mainly terrestrial affinities, is assigned the label "maritime", a term already applied by terrestrial ecologists. The area inhabited by organisms with a preponderantly under-water distribution is called the "sublittoral zone". If a part of this area is occasionally exposed by extremely low tides and wave suck-back, and has a characteristic flora and fauna, it may be considered the "sublittoral fringe".

The area between the maritime and the sublittoral is the "littoral zone", an area characterized by the presence of marine organisms that are adapted to extended exposure to air. The littoral zone may then be divided into sub-zones.

Lewis has divided the littoral into two parts: the eulittoral which extends from the sublittoral to the upper barnacle line, and the littoral fringe which extends from the upper barnacle line to the maritime zone.

Other divisions have been postulated. Of interest are the divisions used by Knox (1960) for the shores of the Southern Hemisphere. Though the labels are sometimes different, the boundaries chosen are easily comparable. The littoral zone of Knox occupies the same range as that of Lewis's eulittoral zone and is divided again into three parts: upper littoral, midlittoral, and lower littoral. The sublittoral also corresponds to the sublittoral of Lewis and Knox is similarly chary of the use of the term sublittoral fringe, both authors showing a preference to speak of the upper sublittoral zone. The main difference in terminology comes in labelling the area above the barnacle line. Knox used the Stephenson supralittoral zone and subdivided it into an upper supralittoral and lower supralittoral. Lewis has rejected the supralittoral term on the grounds that it is semantically misleading and that the area is really one with the littoral. His littoral fringe corresponds with the lower supralittoral of Knox. The lichen zone above the littorinid/Verrucaria population which Knox described as upper supralittoral is designated by Lewis as a part of the terrestrial maritime zone.

ii. As the littoral zone lies largely between tide marks and

its vertical range is largely determined by the range of the tides, it is convenient to use certain tidal levels as points of comparison. These are not used as an absolute unit of measurement so much as a means of dividing various shores into a comparable number of vertical parts with one common physical characteristic so that other characteristics can be compared. The following levels have been used in this paper and are usually expressed by their initials.

EHWS - Extreme High Water Springs, the highest point reached by tides during 1962-64, according to the predictions of the Admiralty Tide Tables (Admiralty 1962, 1963, 1964).

MinHWS - Minimum High Water Springs - the predicted level of the high spring tide of the least range. This term is not common but was felt to be more expressive than the more common Mean High Water Spring, a point that varies because it is calculated on the levels of two successive spring tides. This point, MinHWS, was also found to be more intermediate between EHWS and EHWN (the next term to be defined) and more significant in discussing distribution of organisms.

EHWN - Extreme High Water Neaps, the level predicted for the lowest high tide for 1962-64.

MTL - Mean Tide Level

ELWN - Extreme Low Water Neap, the level predicted for the highest low tide of 1962-64.

MinLWS - Minimum Low Water Springs, the highest low water predicted for any monthly spring tide. This term was invented for the same reasons MinHWs was invented.

ELWS - Extreme Low Water Springs, the level of the lowest predicted tide of 1962-64.

Pier 0 - The Zero point on the tide staff on the New Wharf. This point has not yet been related to any surveyed point on the shore. To date, there is no constant Datum Point for Kaikoura.

It is stressed that all of the above levels are based upon the predicted tide levels, which are calculated on the Lyttelton Datum, and bear little relation to the actual height reached by the water on any given day though averages and maximums based upon these predictions are probably quite close.

iii. Various terms, generally associated with terrestrial ecology, have been applied to intertidal organisms, i.e. association, community, biome, etc. It was felt that it is possible, even desirable, to describe the distribution, habitats, and inter-relationships of the shore organisms of such a limited locale without reference to these terms.

A Check-list of Organisms

The following list is not intended to be a definitive list of the intertidal organisms of the Kaikoura Peninsula. It is a list that contains the names, and authors of the names, of organisms discussed in this paper and of other organisms found on or about the Peninsula. In this capacity it may serve as a guide to others intending to work at this place, or on these organism. As the taxonomic problems involved in identifying so many organisms, from such a diversity of groups, are beyond my solution, a number of experts were consulted. These have been acknowledged earlier. It is customary for the author of such a paper as this to absolve his authorities of all responsibility for the accuracy of determinations and to accept the burden of responsibility for all errors. This, I cheerfully accept, while warning taxonomists and biogeographers alike that these identifications must be considered tentative, in the bulk, particularly in the case of the red algae, and near-microscopic fauna. Certain groups have been entirely ignored because of inability to make identifications.

i. This list of plants contains the names of many species not found growing on intertidal rocks. These are indicated as Drift specimens and are included because they are unlikely to be recorded for this locality. In general, microscopic forms have not been included in this list.

ii. Myxophyta

Rivularia australis Harv.

Oscillatoria sp.

iii. Chlorophyta

Caulerpa brownii Endlich.

Chaetomorpha darwinii (Hook) Kutz.

Cladophora colensoi Harv.

Codium adhaerens C. Ag.

Codium fragile (Suringar) Hariot

Derbesia sp.

Enteromorpha sp.

Sporocladopsis novae-zelandiae*Chapm.

Ulva sp.

iv. Rhodophyta

Abroteia suborbiculata*(Harv.) J. Ag.

Acrochaetium sp.

Antithamnion applicatum*(H. & H.) J. Ag.

Antithamnion ?confusum J. Ag.

Arthrocardia sp.

Asparagopsis armata (Harv.) Schm. Drift

Ballia scoparia Harv.

Ballia scorpoides Mont.

Bostrychia arbuscula H. & H.

Brognartiella sp.

Callithamnion sp.*

Callophyllis calliblepharoidos J. Ag. Drift

Centroceras clavulatum (J. Ag.) Mont.

Ceramium uncinatum H. & H.

Ceramium sp.*

Chaetangium sp.

Champia novae-zelandiae H. & H.

Choreonema sp.*

Cladyhymenia oblongifolia H. & H.

Corallina officinalis L.

Craspedocarpus erosus (H. & H.) Schm.

Crodelia sp.

Crouania ?attenuata (C. Ag.) J. Ag.

Curdiae coriaceae (H. & H.) J. Ag. Drift

Curdiae sp. Drift

Delesia elegans Lamour. Drift

Dipterosiphonia sp.*

Echinothamnion hookeri (Harv.) Kylin

Echinothamnion hysterix (H. & H.) Kylin

Echinothamnion lyalli (H. & H.) Kylin

Echinothamnion mallardiae (Harv.) Kylin

Epymenia obtusa Kutz

Epymenia wilsonis Sond.

Euptilota formossissma (Mont.) Kutz. Drift

Euzoniella incisa* (J.Ag.) Falk.

Falkenbergia rufolanosa* (Harv.) Schm. Drift

Gelidium caulacantheum J. Ag.

Gigartina angulata J. Ag.

Gigartina apoda J. Ag.

Gigartina atropurpurea J. Ag.
Gigartina decipiens H. & H.
Gigartina longifolia J. Ag.
Gigartina rubens J. Ag.
Gracilaria sp.
Grateloupia intestinalis (H. & H.)
Griffithsia antarctica H. & H.
Gymnocongrus nodiferous (C. Ag.) J. Ag.
Herposiphonia sp.
Hymenena palmata (Harv.) Kylin Drift
Hymenena sp. Drift
Hymenocladia lanceolata J. Ag.
Jania ?rubens (L.) Lamour.
Laingia hookeri (Lyall) Kylin Drift
Laurencia sp.
Lenormandia chauvinii Harv.
Lithophyllum sp.
Lophurella sp.
Melanthalia abscissa H. & H.
Melobesia spp.
Microcolax ?botryocarpa*Schm.
Myriogramme crispata* (H. & H.) Kylin Drift
Myriogramme multinervis (H. & H.) J. Ag. Drift
Myriocladia lindaueri Kylin Drift
Myrionema stangulans*Grev.
Nemalion sp.
Nemastoma sp. Drift
Nitophyllum sp. Drift
Phycodrys sp. Drift

Pleonosporium hirtum H. & H.
Pleonosporium sp.
Plocamium abnorme H. & H. Drift
Plocamium angustum (J. Ag.) H. & H. Drift
Plocamium brachiocarpum Kutz. Drift
Plocamium costatum (J. Ag.) H. & H. Drift
Plocamium dilatatum J. Ag. Drift
Polysiphonia cancellata H. & H.
Polysiphonia infestans Harv.
Polysiphonia sp.
Porphyra columbina Mont.
Porphyra subtumens* J. Ag.
Pterocladia lucida J. Ag.
Rhizopogonia sp. Drift
Rhodophyllis gunnii Harv. Drift
Rhodymenia sp. Drift
Schizoseris sp. Drift
Schizymenia novaezelandiae J. Ag. Drift
Streblocladia neglecta Schm.
Trematocarpus acicularis (J. Ag.) Kylin
Warrenia comosa Harv.

v. Phaeophyta

Adenocystis utricularis* (Bory) Skottsb.
Carpomitra costata (Stackh.) Batt.
Carpophyllum maschalocarpum (Turn.) Grev.
Colpomenia sinuosa*(Roth) Derb. & Sol.
Corynophloea cystophorae* J. Ag.
Corynophloea sp.

Cystophora retroflexa (Labill.) J. Ag.
Cystophora scalaris J. Ag.
Cystophora torulosa (R.Br.) Descaine
Desmerestia firma (J. Ag.) Skottsb. Drift
Dictyota ocellata J. Ag.
Durvillea antarctica (Chamisso) Hariot
Durvillea willana Lind.
Ecklonia radiata (C. Ag.) J. Ag.
Ectocarpus confervoides (Roth) Le Jolis
Ectocarpus sp.
Glossophora kunthii (C. Ag.) J. Ag.
Halopteris spicigera (Aresch.) Moore
Halopteris sp.
Haplospongidium saxigenum Lind.
Hormosira banksii (Turn.) Decaisne
Landsburgia quercifolia (H. & H.) Harv.
Leathesia difformis* (L.) Aresch.
Lessonia variegata J. Ag.
Macrocystis pyrifera (L.) C. Ag.
Marginariella boryana (Rich.) Tandy
Marginariella urvilliana (Rich.) Tandy
Microzonia velutina (Harv.) J. Ag.
Myriogloea lindauerri Kylin
Notheia anomala* Bail. & Harv.
Papenfussiella lutea Kylin
Petalonia sp.
Ralphsia verrucosa (Aresch.) J. Ag.
Sargassum sinclairii H. & H. Drift
Scytosiphon lomentaria (Lyngb.) J. Ag.

Scytothamnus australis (J. Ag.) H. & H.
Scytothamnus fasciculatus (H. & H.) Cotton
Splanchnidium rugosum (L.) Grev.
Tinocladia novae-zelandiae Kylin

* denotes an epiphyte

i. The list of animal species differs from the algal list in many ways. Only animals collected on the rocky shores of the Kaikoura Peninsula have been included. Sand and mud dwellers have been excluded as well as free swimming and subtidal forms. These measures have been taken to keep the list to a practical length, to keep it in line with the topics discussed in the paper, and because there are many zoologists working in the area who will be producing more detailed lists of certain groups. Therefore, it was felt that there was no urgency in publishing a longer list.

ii. Coelenterata - Hydrozoa

Staurocladia vallentini Browne

Obelia sp.

iii. Coelenterata - Actinozoa

Actinia tenebrosa Farq.

Actinothoe albens Stuck.

Actinothoe albocincta Hutton.

Anthopleura aureoradiata Stuck.

Anthopleura minima Stuck. & Walton

Cricophorus nutrix Stuck.

Edwardsia tricolor Stuck.

Epiactis thompsoni Cough.

Isocradactis magna Stuck.

Isoparactis ferax Stuck.

Oulactis mucosa Drayton

Phlyctenactis tuberculosa Quoy & Gaim.

iv. Platyhelminthes - Turbellaria

Leptoplana brunnea Cheese

v. Annelida - Polychaeta

Abarenicola affinis Wells

Cirriformia tentaculata Mont.
Eualia microphylla Schmarda
Eunice australis Quatr.
Glycera sp.
Lepidonotus polychromus Schmarda
Nereis sp.
Odontosyllis sp.
Orbinia papillosa Ehlers
Perinereis ambylodonata Ehlers
Perinereis nuntia Savigny
Pomatoceros cariniferus Gray
Spirorbis zelandica Gray
Syllis sp.
Thelepus sp.
Trypanosyllis sp.

vi. Annelida - Sipunculoidea
Dendrostoma huttoni Benham
Phascalosoma annulatum Hutton
Phascolosoma sp.

vii. Arthropoda - Cirrepedia
Balanus sp.
Calantica villosa Gray
Chamaesipho brunnea Moore
Chamaesipho columna Spengler
Elminius plicatus Gaim.
Pollicipes sertus Darwin
Pollicipes spinosus Quoy & Gaim.
Tetraclita purpurescens Wood

viii. Arthropoda - Isopoda

Ampharoidea falcifer Thomp.
Cirolana australiensis Hale
Cirolana pellucida Tatt.
Cymodoce bituberculata Filhol.
Cymodoce cordiforaminalis Chilt.
Euidotea peronii Milne-Edw.
Isocladus armatus A. Milne-Edw.
Isocladus magellanicus Richardson
Isocladus spiniger Dana
Leptanthura chiltoni Bedd.
Paridotea ungulata Pallas
Plakarthrium typicum Chilt.
Serolis paradoxa Fabr.

x. Arthropoda - Decapoda

Bateus aequimanus Dana
Jasus lalandii Milne-Edw.
Palaemon affinis A. Milne-Edw.

Petrocheles spinosus Miers
Petrolisthes elongatus Milne-Edw.
Cancer novae-zelandiae Jacq.
Cyclograpsus lavauxi Milne-Edw.
Elamena producta Kirk
Elemena sp.
Hemigrapsis edwardsii Hilg.
Heterozius rotundifrons A. Milne-Edw.
Liocarcinus corrugatus Pennant
Ovalipes punctatus de Haan
Notomithrax minor Filhol.
Notomithrax ursus Herbst.
Pilumnus novae-zelandiae Filhol.

xi. Arthropoda - Arachnida
Desis marina Hector
Ixeuticus martius Simon

xii. Mollusca - Amphineura
Acanthochiton zelandicus Quoy & Gaim.
Amaorochiton glaucus Gray
Eudoxochiton nobilis Gray
Frembleya egregia H. Adams
Ischnochiton maorianus Iredale
Maorochiton sp.
Onithochiton neglectus Roche
Sypharochiton pelliserpentis Quoy & Gaim.
Sypharochiton sinclairi Gray

xiii. Mollusca - Prosobranchiata
Atalacmea fragilis Sowerby
Buccinulum sp.

Cantharidella sp.
Cantharidus opalus Martyn
Cantharidus sp.
Cellana denticulata Martyn
Cellana Flava Hutton
Cellana ornata Dillwyn
Cellana radians Gmelin
Cellana strigilis Hombron & Jacq.
Cominella adspersa Bruguiere
Cominella mucosa Martyn
Eatoniella olivacea Hutton
Eatoniella delli Ponder
Eatoniella noalabia Ponder
Emarginula striatula Quoy & Gaim.
Estea rekohuana Powell
Haliotis australis Gmelin
Haliotis iris Martyn
Haliotis virginea Gmelin
Haurakia hamiltoni Suter
Haustrum haustorium Gmelin
Herpetopoma bella Hutton
Lepsiella albomarginata Desh.
Lepsiella scobina Quoy & Gaim.
Leuconopsis obsoleta Hutton
Liotella Polypleura Hedley
Lunella smaragda Gmelin
Maoricrypta monxyla Lesson
Melagraphia aethiops Gmelin
Melaraphe cincta Quoy & Gaim.

Melaraphe oliveri Finlay
Merelina lyalliana Suter
Michrelenchus sp.
Notoacmea daedala Suter
Notacmea parvaconoides Suter
Notoacmea scopulina Oliver
Patelloida corticata Hutton
Risselopsis varia Hutton
Rufodardanula exigua Ponder
Scrobs hedleyi Powell
Scutus breviculus Blain.
Sigapatella novae-zelandiae Lesson
Skenella pfefferi Suter
Trochus tiaratus Quoy & Gaim.
Zeacumantus subcarinatus Sowerby
Zediloma atrovirens Philippi
Zediloma digna Finlay
Zemitrella choana Reeve

xiv. Mollusca - Opishthobranchiata

Aeolidiella drusilla Bergh.
Aeolidia gracilis Kirk
Aglaja cylindricus Cheese.
Benhamina obliquata Sowerby
Doris lanuginata Abraham
Pleurobranchiae novae-zelandiae Cheese.

xv. Mollusca - Pulmonata

Onchidella flavescens Wissel
Siphonaria novae-zelandiae Quoy & Gaim.

xvi. Mollusca - Lamellibranchiata

Aulocomya maoriana Iredale
Lasea hinemoa Finlay
Hiatella australis Lamarck
Modiolaria barbata Reeve
Modiolus neozelanicus Iredale
Mytilus edulis L.
Notcorbula zelandica Quoy & Gaim.
Pachykellia minima Powell
Perna canaliculus Gmelin
Zelithophaga truncatus Gray
Zemyllita stowei Hutton

xvii. Mollusca - Cephalopoda
Octopus maorum Hutton
Robsonella australis Hoyle

xviii. Echinodermata - Asteroidea
Coscinasterias calamaria Gray
Patiriella regularis Verrill
Stichaster australis Mull. & Tros.

xix. Echinodermata - Ophuroidea
Amphipholis squamata Delle Chiaje
Amphiura amokurae Mortensen
Ophionereis fasciata Hutton
Ophioteris antipodum Smith

xx. Echinodermata - Echinoidea
Evechinus chloroticus Valenc.

xxi. Echinodermata - Holothuroidea
Ocnus calcarea Dendy
Protankyra uncinata Hutton
Stichopus mollis Hutton

Trochodota dunedinensis Parker

xxii. Protochardata - Urochorda

Pyura pachydermatina Herdman

Biological description of shore areas

Laboratory Rocks (Pl. 6) (Fig. 8)

The rocky shore that extends from below the Edward Percival Marine Laboratory to the New Wharf represents the only part of the northwest face of the peninsula that is exposed to the sea. Large limestone outcroppings dominate the intertidal. There are many cracks, crevices and overhangs in the area. Tongues of shingle, silt, sand, and small stones intrude to separate the rocks of the upper shore from the outer lower rocks.

A high shingle bank separates the intertidal region from the terrestrial environment. The maritime zone is represented by the edges of the cultivated roadway.

Upper levels of the highest outcroppings support the littorinids, Melaraphe cincta and M. oliveri and, in some places, the golden lichen that is characteristic of the littoral fringe.

Throughout the littoral, numerous shaded clefts and small pools affect the picture of the vertical zonation. Deep clefts run perpendicular to the shore, forming surge channels that are steep walled and narrow and thus receive only the late afternoon sun. Here, the rock is seldom truly dry and the "effective tide level" is considerably higher than the true level.

The banding of organisms is not as disecrete and obvious as at other points on the peninsula. The apparent discontinuities in distributions are due to the extreme irregularity of the substrate. A close examination shows that there is a clear pattern of banding if comparable surfaces are studied with an eye to their vertical relation and ignoring horizontal discontinuities.

The banding of the major species is shown on Fig. 8. Not shown in the figure are the many crevice dwellers such as Sypharochiton pelliserpentis and Onchidella flavescens which are common and the less abundant mussels, Aulacomya maoriana and Mytilus edulis, nor the shade forms, like Ralfsia verrucosa which lines the crevice walls.

The shingle and silt beds have a large under rock fauna of stone crabs, Petrolisthes elongatus, chitons, Amaorochiton glauca and Ischnochiton maorianus, the cushion star, Patiriella regularis, the small tube worm, Spirorbis zelandica, and a solitary tunicate.

Among the less frequent inhabitants of the area are the whelks, Haustrum haustorium and Lepsiella scobina, and the wandering anenome, Phlyctenactis tuberculosa, which crawls over the Hormosira banksii and Cystophora torulosa. H. banksii forms a wide band in the lower eulittoral. C. torulosa occupies the lowest part of the eulittoral, its upper limit slightly overlapping the lower limit of H. banksii.

Heavily silted areas have permanent beds of eel-grass, Zostera sp. with its associated burrowing forms.

Closer to the New Wharf, the intrusions of silt and shingle diminish and the rock faces are more continuous and uniform. The banding of organisms becomes more obvious and discrete. There is also a gradual increase in wave action from the Laboratory Rocks to the New Wharf. The Chamaesipho columna band becomes more concentrated and wider while the Hormosira band becomes narrower. Below the Hormosira, a turf of small algae occurs. The composition of the turf varies with the season and the place but the predominant species are Echinothamnion spp., Champia novae-zelandiae, and Halopteris spicigera.

As the wave action increases Cystophora torulosa is replaced by Carpophyllum maschalocarpum.

Wakatu Point (Pl. 8)

At Wakatu Point, the maritime zone terminates sharply at the top of a shingle bank. Below this bank, the sharply folded limestone rocks of the intertidal form a gently sloping platform that extends below the low water mark on both sides of the point but drops off more sharply within the lower intertidal near the tip. Near the tip of the point the platform is dissected by many small channels so that there are many surfaces exposed to different degrees of wave action, light, etc. Reference to Fig. 8 shows that this point is subject to a wide range of wave action.

Generally, the littoral fringe is somewhat truncated at Wakatu Point. Some of the larger limestone outcrops may carry to the upper limit of the fringe, this would be hard to judge. At the flanks of the point, the rock surfaces do not extend high enough to be littoral fringe. The littoral fringe and upper eulittoral have a concentrated population of Melaraphe spp. The upper boundary of the eulittoral is marked by an irregular barnacle population that consists of varying proportions of Chamaesipho columna, C. brunnea, and Elminius plicatus. In the eulittoral, the barnacles and Melaraphe spp. have distributions that overlap with a mixed gastropod population. Particularly common throughout the upper eulittoral are Cellana spp., Siphonaria novae-zelandiae and Sypharochiton pelliserpentis. Somewhat lower, near the lower limit of the Melaraphe spp. are large numbers of Melagraphia aethiops, even near the exposed end of the point where they find shelter in the many nooks and crannies formed by the limestone folding.

Overlapping the distribution of M. aethiops and extending into the sublittoral zone are numbers of Lunella smaragda.

Anenomes form a substantial part of the fauna of the lower littoral along the flanks of the point. Epiactis thompsoni being the most evident species.

Several sublittoral species may be found, above the low water line, under small ledges formed by the limestone layers. Prominent examples include Scutus breviculus, Haliotis australis, and Hemigrapsis edwardsii.

The algal banding in the lower eulittoral is very complex. Near the base of the point, the seasonal Porphyra columbina dots the rocky ridges and a heavy concentration of Scytosiphon lomentaria fills the crevices.

Hormosira banksii is the highest year around algal band former. The growth of H. banksii is heaviest near the base of the point and is much broken by the varying aspect of the rock surfaces. Mixed with the H. banksii are seasonal blooms of Ectocarpus confervoides and Ceramium spp. Papenfussiella lutea and the epiphytes Colpomenia sinuosa and Leathesia difformis are common in the quieter waters. Cystophora spp. are common near the low water mark.

An algal turf is often evident below the H. banksii, especially towards the tip of the point. Many channels dissect the rock mass and the resultant variety of surface exposures and aspects are reflected in the algal banding. This turf is composed of Gigartina decipiens, Halopteris sp., and Echinothamnion spp. In some places the species are mixed together, in other places they occur as separate patches. In the sheltered channels a band of Caulerpa brownii, or a concentration of Codium adhaerens often occurs.

Below the turf are the brown algae of the lower eulittoral. There may be Cystophora spp., Carpophyllum maschalocarpum or Durvillea antarctica depending upon the exposure to wave action.

The sublittoral zone is marked by patches of Marginariella boryana, Lessonia variegata, Ecklonia radiata, and Macrocystis pyrifera.

Avoca Point, Moa Point, and Waeroa Point (Pl. 7, 17, 18) (Figs. 9 18, 19)

On two sides of the peninsula there are points of striking similarities. On the northeast face there is Avoca Point and on the southwest face are Moa Point and Waeroa Point. These points are formed from the same rock formation, have similar exposures to wave action, and have similar topography. It is not surprising then that the distribution of organisms is similar.

There are hints of a true maritime zone at Waeroa Point and Moa Point where small patches of the ice-plant, Mesembryanthemum edule are found. In the main, the higher rocks lie within the littoral fringe, having a sparse population of Melaraphe spp. and lichen. The eulittoral zone starts with a patchy belt of Chamaesipho columna mixed with a small, spotty black lichen and a thick population of Cellana spp., notably C. radians, C. ornata, and C. denticulata, which does not include many individuals of the larger sizes. Scattered through the limpet band are Sypharochiton pelliserpentis, Onchidella flavescens, and Siphonaria novae-zelandiae.

A marked increase in both flora and fauna is evident in the lower eulittoral. Here, there are many small pools and damp depressions. The pools and depressions have a heavy growth of Hormosira banksii, and numbers of Melagraphia aethiops and Lunella smaragda. Other algae may become prominent in certain pools. Small pools often have a heavy growth of Corallina officinalis with an attendant microfauna. Large pools may have one, or more, of Halopteris spicigera, Cystophora torulosa, C. scalaris Glossophora kunthii or Ulva sp.

Damp spots will often have small growths of Enteromorpha sp. or Scytosiphon lomentaria when these algae are in season.

On the drained seaward slopes the Hormosira band is often thin and patchy. Below it is a thick turf of Halopteris sp. which blends with a lower band of mixed red algae, notably Echinothamnion spp., Champia novae-zelandiae, and Gigartina decipiens. G. decipiens has only been found at Wakatu Point and Waeroa Point though it is a very common species a few miles south of the peninsula. Other red algae are found mixed with this turf in small quantities. Below this turf is a tight band of Carpophyllum maschalocarpum. In certain sheltered nooks the Carpophyllum may give way to Cystophora torulosa. In less sheltered spots where the slope of the rock is steep Carpophyllum may be replaced by Marginariella boryana.

The undergrowth for the upper sublittoral and the lower eulittoral is invariably prostrate elements of Corallina officinalis. Loose stones and large pieces of shingle are often encrusted with Crodelia sp. which is apparently more tolerant of an unstable environment than Corallina.

Wairepo Flats, Mudstone Bay Flats (Figs. 10, 17)(Pls. 9, 10, 16)

The largest total area of intertidal platforms on the peninsula is formed of siltstone. The two largest siltstone platforms are Wairepo Flats on the northeast and the Mudstone Bay Flats on the southwest. These platforms have a very gentle seaward slope, (1:50 - 1:400), for up to two hundred meters. They rise gently at the seaward edge to form a slight parapet effect. At the very edge they round off and drop sharply into the subtidal. Both platforms are topped by shingle banks at just above EHWN. This virtually eliminates the littoral fringe.

There are a few spots on the platform that have an unmixed littorinid population representing the littoral fringe. However, it is very difficult to determine the upper boundary of the eulittoral zone as there are no barnacles on the platforms with the singular exception of a band on some large boulders sitting on Wairepo Flats. By comparison with the barnacles on these boulders and the levels of barnacles in other sheltered areas it was determined that the upper limits of Melagraphia aethiops would serve to delimit the eulittoral littoral fringe boundary. This seemed consistent with the principles of Lewis (1964).

Melagraphia aethiops is the obvious dominant of the upper eulittoral though the less obvious Zeacumantus subcarinatus, which is hidden in pools and crevices during the day, probably surpasses M. aethiops in both numbers and biomass.

The surface of the siltstone is crisscrossed with small grooves, and again divided into larger areas by runnels. In winter, the top of the siltstone is covered with Porphyra columbina which reaches 100% cover in the middle of its range.

Where the cover is less than 100%, as in the grooves and runnels, there are patches of Scytosiphon lomentaria Enteromorpha sp., and Ectocarpus confervoides. In summer this level is bare of macroscopic plant life. On the Mudstone Bay Flats there is a bloom of Rivularia australis, during March and April, that seems more curious than significant.

In the lower eulittoral differences are observed between certain areas of the platforms. These appear to be related to the slight differences in the topography of the sublittoral floor. The sublittoral bed is slightly deeper off the Wairepo Flats than off the Mudstone Bay Flats. This difference is enough to dampen wave action, slightly, allowing silt to collect on the platform at the eastern end of Mudstone Bay.

The Wairepo Flat platform has a wide belt of Hormosira that harbors many other plants and animals. Within the Hormosira band are the lower limit of Melagraphia aethiops, the upper limit of Lunella smaragda, large numbers of Zeacumantus subcarinatus and assorted whelks, the entire range of Epiactis thompsoni and other anenomes, and a dense undergrowth of Corallina officinalis. Near the lower edge of the Hormosira band, and on into the lower band of Cystophora torulosa, the Corallina becomes more dense and harbors many small algae and a mixed fauna of microscopic and near-microscopic forms. Prominent in the fauna of this undergrowth are minute gastropods including: Eatoniella olivacea, Liotella polypleura, Rudfodardanula exigua, Hawkia hamiltoni, Merelina lyalliana, Estea rekohuana, Scrobs hedleyi and Rissoella rissoaformis. Other forms present include Champia novae-zelaniae, Colpomenia sinuosa, Adenocystis utricularis, Leathesia difformis, Lepsia haustorum, and Lepsiella albomarginata.

The Cystophora torulosa band is only exposed at the lowest tides. Other algae found at this level are: Caulerpa brownii which forms a green band on the sheltered side of rocks, Cystophora retroflexa and Cystophora scalaris whose centers of distribution are deeper than that of C. torulosa, and several polysiphonous red algae and attendant epiphytes.

This picture of abundance compares in kind, but not in number, with the lower eulittoral of the Mudstone Flats.

At Mudstone Bay the plant cover has some seasonal distinctions. During the winter months a band of Ulva sp. and/or Enteromorpha sp. is prominent above the Hormosira band. The animal population is of a similar assortment but less dense than that at Wairepo Flats. There are very few plants or animals below the Hormosira as the platform drops sharply to a shingle bottom that is only a few inches below ELWS.

A small area of the platform, near the base of Sharkstooth Point lies lower than the main platform and slopes into the sublittoral. This part of the platform collects considerable silt throughout the Hormosira range and below. The minute gastropods are abundant in the undergrowth of Corallina officinalis which traps mud and silt to form an excellent substrate for burrowing forms. Enteromorpha and Ulva are scattered through the Hormosira rather than forming discrete bands as they do on the upper flats. Below the Hormosira there is a mat of Ceranium sp. that has distinct seasonal fluctuations leaving the Corallina officinalis as the dominant forms for several months. Colpomenia sinuosa is abundant on the Corallina band. Below the Corallina officinalis band the rocks cease being a contiguous platform and are broken up by numerous channels.

At the bottom of the C. officinalis band on these rocks there is often a fine line of Caulerpa brownii, and then a broken band of Echinothamnion spp. Below this turf, which could be considered the bottom of the littoral zone, is the sublittoral floor of loose rock with only Crodelia sp. as an evident plant form.

Lighthouse Point (Pl.13) (Fig. 14)

The platform at Lighthouse Point lies, for the most part, just below EHWN. The seaward edge rises in a parapet effect to EHWS in many places. The outer wall of the platform is constantly subject to heavy wave action whereas the main surface is gently flooded and never subject to violent waves as the water over the platform is too shallow to support more than ripples. The platform surface consists of large, flat, smooth areas of siltstone dissected by runnels and channels.

The only littoral fringe is a narrow line at the base of the cliff where the littorinids are found in an unmixed condition. The platform is mainly upper eulittoral and dominated by a molluscan fauna. Melaraphe spp. and Melagraphia aethiops are to be found in great numbers. The pools and runnels are filled with Zeacumantus subcarinatus. On the back slopes of the seaward parapet a change occurs, Cellana spp. and Siohonaria novae-zelandiae become the dominants with Melaraphe spp. re-appearing on the highest points.

During the summer months the platform is conspicuously bare of macroscopic plant life except for the Corallina officinalis, and sometimes Jania rubens, in the runnels and channels. During the winter the entire platform is covered with Porphyra columbina, which forms pure stands on the well drained slopes, and with Scytosiphon lomentaria, which mixes with the Porphyra columbina in damp spots and forms pure stands in pools. Minor winter growths include Cladophora sp., Ectocarpus confervoides, and Entermorpha sp.

The seaward slopes are quite steep and evidence a discrete banding.

The upper half, to two-thirds, has a good cover of the barnacles, Chamaesipho brunnea, C. columna, and Elminius plicatus. Mixed with the barnacles are Melaraphe spp., Risselopsis varia and Cellana spp. Near the lower edge of the barnacle band, a thin intermittent line of Splanchnidium rugosum occurs. Below the barnacles the prostrate form of Corallina officinalis and the molluscs, Cellana spp. Patelloida corticata, and Siphonaria novae-zelandiae are most evident. In early summer a band of Chaetangium corneum dots the upper Corallina officinalis.

The presence, and composition, of a mixed algal turf near the bottom of the littoral is dependent upon the slope and exposure of the rock face. Where the turf exists, it is largely composed of Halopteris sp. and Echinothamnion spp.

The lowest exposed surfaces may be marked by Carpophyllum maschalocarpum, Marginariella boryana, or Durvillea antarctica depending upon slight changes of slope and exposure.

Seal Reef and Wooloomooloo Channel (Pls. 11 & 12) Figs. 12, 13)

Seal Reef is an extension of Lighthouse Point, from which it is separated by the shallow depression of Wooloomooloo Channel whose bottom is just below ELWS. The channel bottom, though never exposed, has a littoral flora. Sublittoral animals come and go, mixing with forms that are found in the littoral zone. On each side of the channel there is a narrow band of Hormosira banksii. Codium adhaerens is common on the rocks of the western side of the channel and a periodic growth of Ulva sp. marks the north end of the eastern side. Above this level the flora and fauna are those of the platforms.

The reef slopes upward and outward to the North-east. Along the northwestern face of the reef there is a continual increase in height and of exposure to wave action (Figs. 6 12). These faces and slopes exhibit a band of barnacles in which the concentration of Chamaesipho columna lessens as the wave action increases, the concentration of Chamaesipho brunnea becomes greater - then less, and the concentration of Elminius plicatus increases until there are nearly pure stands of E. plicatus at the most exposed points. As the wave exposure increases the barnacle band widens.

Below the barncles there is a band of mixed algal turf. As the wave action increases this band consists entirely of Halopteris sp. and Corallina officinalis. At the exposed eastern end of the reef the Halopteris disappears also. In this more exposed region, Carpophyllum maschalocarpum disappears and is replaced by first Durvillea antarctica which is in turn replaced by Durvillea willana.

Deep channels have formed between rock masses on the reef. In these surge channels, the Corallina officinalis level is raised considerably and the Carpophyllum maschalocarpum is mixed with the sublittoral species, Marginariella boryana, Lessionia variegata, Ecklonia radiata, and Macrocystis pyrifera.

The surface of the reef can be considered as a series of raised platforms. The upper level, at the northwestern and eastern edges, has an unmixed population of Melaraphe spp. and can be considered littoral fringe. The next level, just central to the above, has extensive beds of Modiolus neozelanicus. These are the only large stands of Modiolus on the peninsula. Most of the reef surface lies at the next level which has Cellana spp. and Melagraphia aethiops as obvious dominants and is, generally speaking, the same as the Lighthouse Point platform.

The southern tip of the reef is formed by a massive limestone outcropping which serves as a nesting site for the Red-billed Gull and as a residence for a number of Fosters' Seals. This area was not extensively surveyed but general observations indicate that the distinctive feature is the presence of pools with a high nitrogenous content and a correspondingly high growth of Enteromorpha spp., other Chlorophyta, and Tigriopus sp.

Sharkstooth Point (Pls. 14, 15) (Figs. 15, 16)

Sharkstooth Point extends from the southern corner of the peninsula in much the same manner as Lighthouse Point and Seal Reef extend from the eastern corner. The intertidal platform is siltstone and has a high ridge along the eastern edge and southern tip. These high points support an unmixed population of Melaraphe spp. A slightly lower surface supports a very small patch of Modiolus neozelanicus. Below that the main level of the platform has a heavy population of Melagraphia aethiops and Cellana spp. Other grazing gastropods are found in limited numbers. Crevices harbor large numbers of Zeacumantus subcarinatus. During the winter most of the reef is covered with Porphyra columbina.

The southern tip of the reef consists of large separate masses of rock. Here there are back slopes, caves, channels, overhangs, and numerous surface irregularities. This area also receives a maximum wave action. Well developed bands of Elminius plicatus and Chamaesipho brunnea extend four to five feet on vertical faces. Actinia tenebrosa is abundant where wave action is broken. The channels are clogged with Durvillea spp., Carpophyllum maschalocarpum, Macrocystis pyrifera, and Marginariella boryana. During spring tides, in calm weather, the caves and overhangs can be examined. The population of tunicates and sponges that abound in the dark wet places are truly sublittoral.

The eastern edge of the platform is more discrete. The zonation is similar to that of the southern tip except that the barnacles are less dense and a larger proportion of Chamaesipho columna is included.

Points of the southeast face

The three major points of the southeastern face of the peninsula have basically the same structure and exposure. All are sharp-edged limestone at the base, and are capped with substantial masses of siltstone at the tips. Each has a ledge of shingle that separates the rocky intertidal from the terrestrial maritime zone. Each bay between the points has a coarse shingle bottom and beach.

Only the low eulittoral is represented by a rock substrate near the base of the points. A large quantity of heavily silted Corallina officinalis forms and undergrowth for the Cystophora spp., Ulva sp. and Hormosira banksii. Pools collect great quantities of algal drift and the Cystophora spp. are heavy with epiphytes. Other species represented are: Codium adhaerens, Dictyota ocellata, Scytosiphon lomentaria, small red algae, Melagraphia aethiops, and Cellana spp.

Further seaward, the banding becomes more distinct. The Cystophora spp. are topped by a band that consists mainly of Echinothamnion spp., Gigartina angulata, and Streblocladia neglecta. Above the algal turf there is a heavy population of Siphonaria novae-zelandiae, Patelloida corticata, and Cellana spp. mixed with a small number of Chamaesipho columna. Less prominent are Splanchnidium rugosum, Scytothamnus australis, Lunella smaragda, Melagraphia aethiops, and Melaraphe spp.

Near the end of the points, Carpophyllum maschalocarpum comes up into the eulittoral to form a definite band. The mixed algal turf separates into sub-bands.

Sub-bands may consist of: Halopteris spicigera, H. congesta, Echinothamnion hystrix, E. mallardiae, Laurencia sp., Gracilaria sp., and Champia novae-zelandiae.

At the exposed tips of the points, Durvillea antarctica forms a four to five foot band topped by a nearly pure stand of Elminius plicatus. Limpets are the most evident mobile species, of which Cellana denticulata is the most prominent.

Plate 6.

Laboratory rocks from the cliff above the Edward Percival Marine Laboratory (lower left). The intrusion of gravel and sand flats between the limestone is clearly shown. Taken just before low water. (Photograph J.T. Darby, 23 December 1964).

Plate 7.

The zonation at the end of Avoca Point. This photograph was taken during a spring low tide, at the moment of wave suck-back. A line of Marginariella boryana is evident at the waters edge marking the upper boundary of the sublittoral zone. Above the M. boryana is a small band of Cystophora torulosa. Above the C. torulosa is a band of Echinothamnion sp. Scattered individual plants of Hormosira banksii may be seen. The low density of barnacle cover is evident.

Note the division of substrate from siltstone on the left to limestone on the right. (Photograph J.T. Darby, 7 November 1965.)

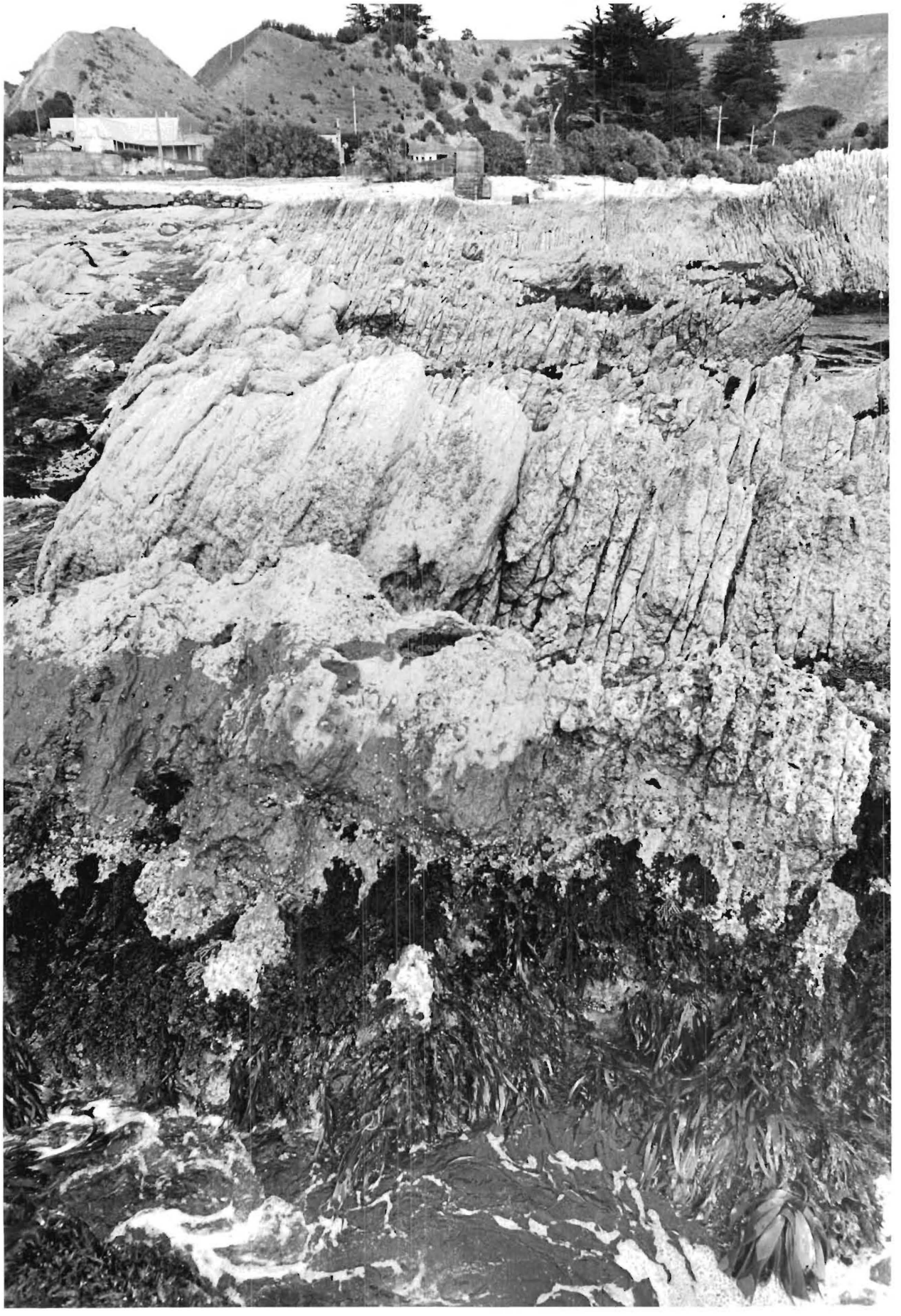


Plate 8.

Wakatu Point viewed from the top of the peninsula. This photograph was taken during a low spring tide. It shows the surface irregularity of the limestone points and the diminishing wave effect from tip to bay. (Photograph R.A. Rasmussen, 7 April 1965).

I. C. 4. d.

Plate 9.

Wairepo Flats seen from the bluff over the Old Wharf. This photograph shows the extent of the siltstone platforms and the gentle slope. The darker areas are beds of Hormosira banksii. (Photograph R.A. Rasmussen, 7 April 1965).

Plate 10.

The winter zonation of Wairepo Flats. The uppermost growth is the seasonal Porphyra columbina. Immediately below the P. columbina is a band of Hormosira banksii. Below the H. banksii is a band of Cystophora torulosa extending below the water line. Taken at low water between neap and spring tides. (Photograph R.A. Rasmussen, July 1964).

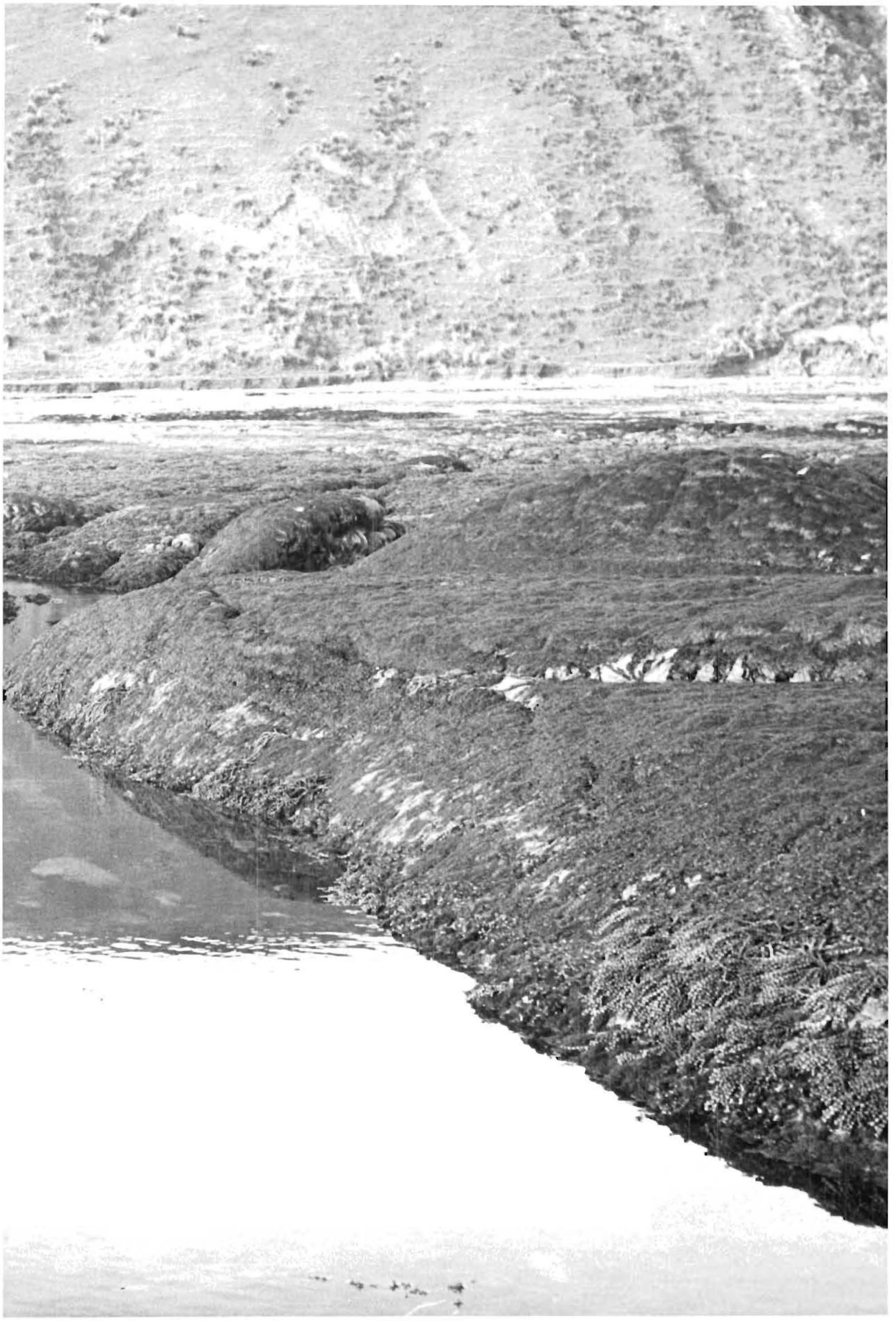


Plate 11.

Zonation on Seal Reef near the end of transect 4, on the northeast side of the reef. The depth and concentration of the barnacle belt may be clearly seen. The algal banding is somewhat mixed. For the most part, the turf is composed of patches of Halopteris sp. and Echinothamnion sp. At the bottom of the turf, individual Lessonia variegata and Marginariella boryana can be distinguished. Taken shortly after low water during spring tides. (Photograph J.T. Darby, 7 November 1964).

Plate 12.

The zonation pattern at the end of transect 5, Seal Reef - East. The pattern is shifted upward by a channel effect. The light areas above the Durvillea willana are prostrate elements of Corallina officinalis. The barnacles are almost entirely Elminius plicatus. The limpets are Cellana denticulata. Taken during the wave suck-back during a low spring tide. (Photograph J.T. Darby, 7 November 1968).

Plate 13.

A view of the edge of the Lighthouse Point platform near transect 7. Taken just after low water of a neap tide. (Photograph J.T. Darby, 1 May 1965).

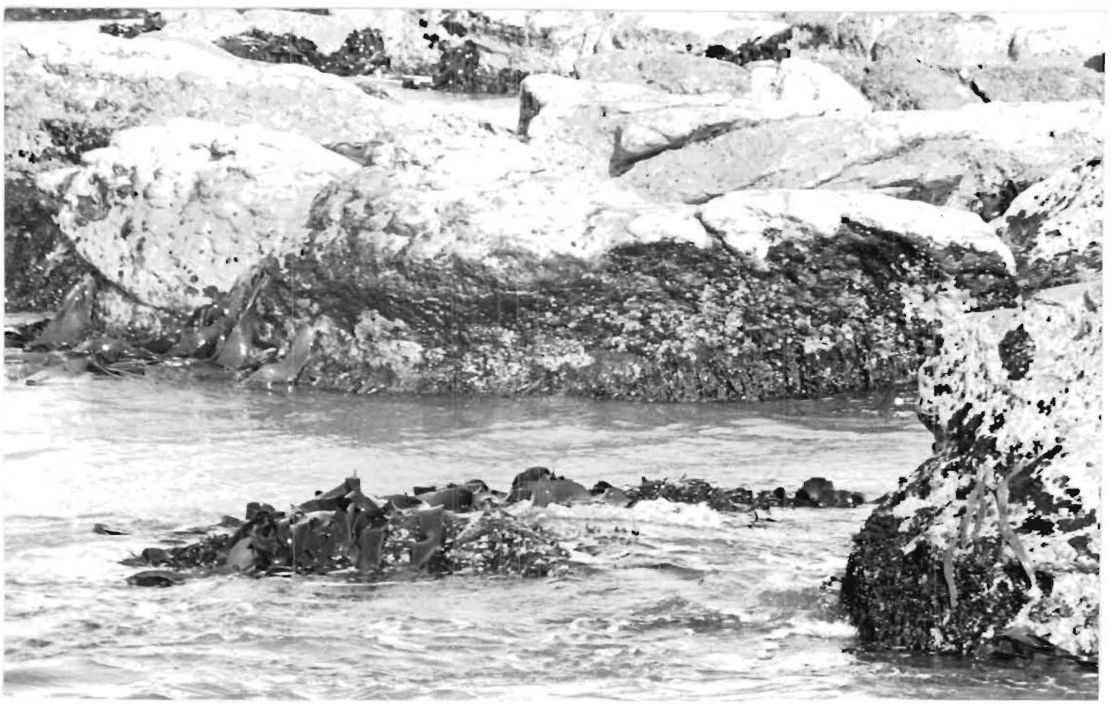


Plate 14.

The eastern edge of the Sharkstooth Point platform near the end of transect 8. Taken at the low water of a neap tide, from the bluffs above the point, with a 350 mm. lens. (Photograph J.T. Darby, 1 May 1965).

Plate 15.

The western edge of Sharkstooth Point near the end of transect 9. The narrow algal band of the lower eulittoral is just submerged. A small patch of Porphyra columbina is developing on the upper rock surfaces at the left. Below this level, the rocks are nearly bare except for a few barnacles and limpets. However, crevice dwellers are abundant. (Photograph J.T. Darby, 1 May 1965).

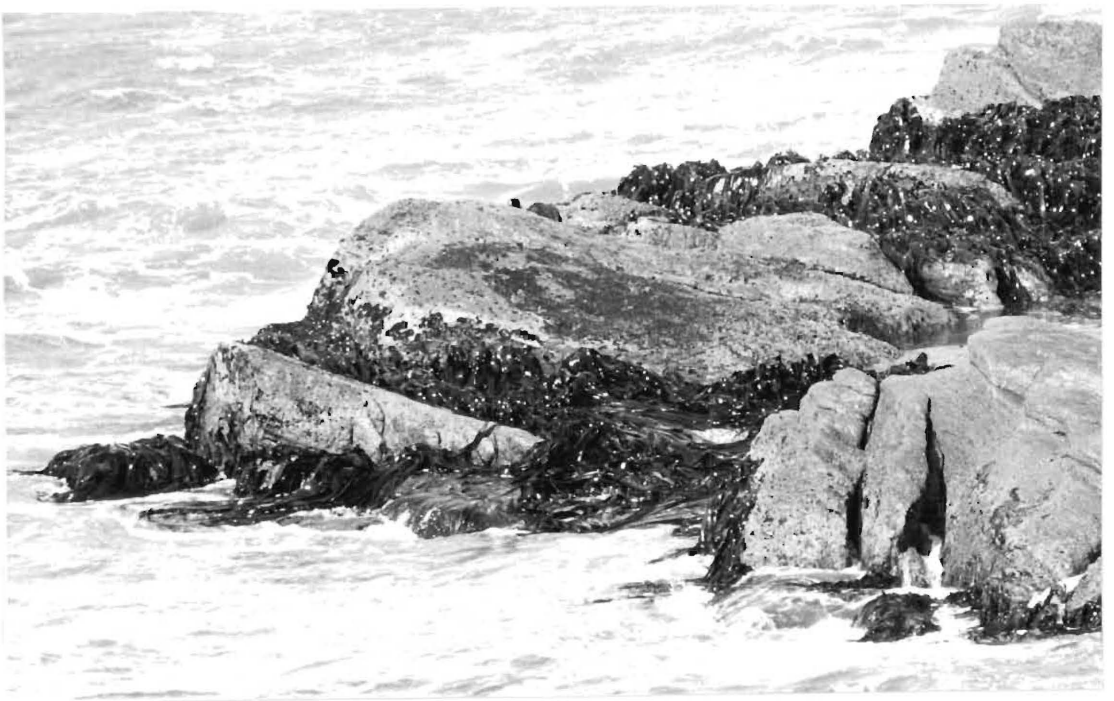


Plate 16.

Mudstone Bay Flats viewed from the bluff. The similarity between these flats and Wairepo Flats (Pl. 9) is evident. Taken at low water of a spring tide. (Photograph R.A. Rasmussen, 7 April 1965).

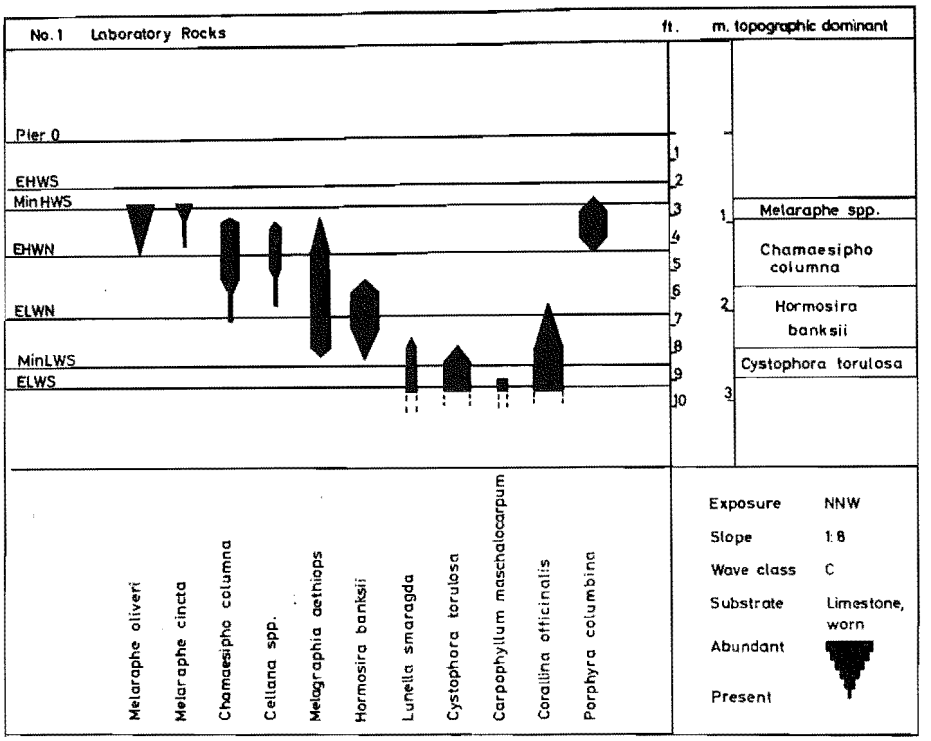
I. C. 4. c.

Plate 17.

A view of Limestone Bay and Waeroa Point showing the similarity with Wakatu Point (Pl. 8). The rock mass in the upper left is known as Baxter's Reef and is not figured on the maps in this paper. (Photograph R.A. Rasmussen, 7 April 1965).

Plate 18.

Rocks near the end of transect 12, Waeroa Point - Southwest. The photograph shows the extreme folding of the limestone layers. The spotty algal growth above the Hormosira banksii band is a remnant of the previous season's Porphyra columbina. (Photograph J.T. Darby, 7 November 1964).


No. 1 Laboratory Rocks
ft.
m. topographic dominant
Pier 0
EHWS
MinHWS
EHWN
ELWN
MinLWS
ELWS
1
2
3
4
5
6
7
8
9
10
1
2
3
Melaraphe spp.
Chamaesipho columna
Hormosira banksii
Cystophora torulosa
Melaraphe oliveri
Melaraphe cincta
Chamaesipho columna
Cellana spp.
Melagraphia aethiops
Hormosira banksii
Lunella smaragda
Cystophora torulosa
Carpophyllum maschalocarpum
Corallina officinalis
Porphyra columbina
Exposure NNW
Slope 1:8
Wave class C
Substrate Limestone, worn
Abundant
Present

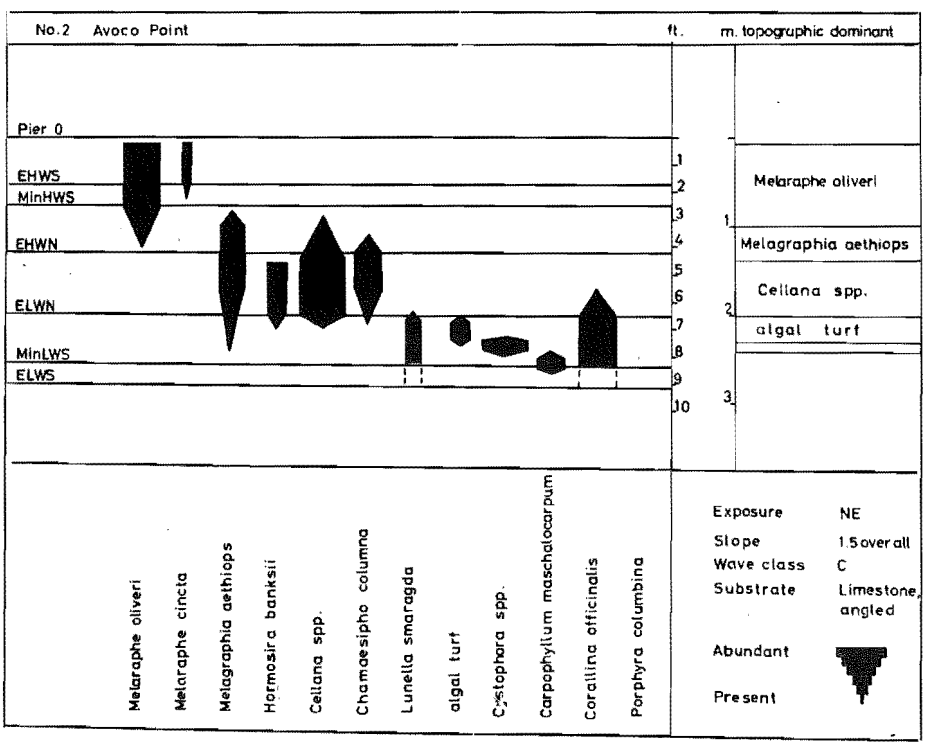
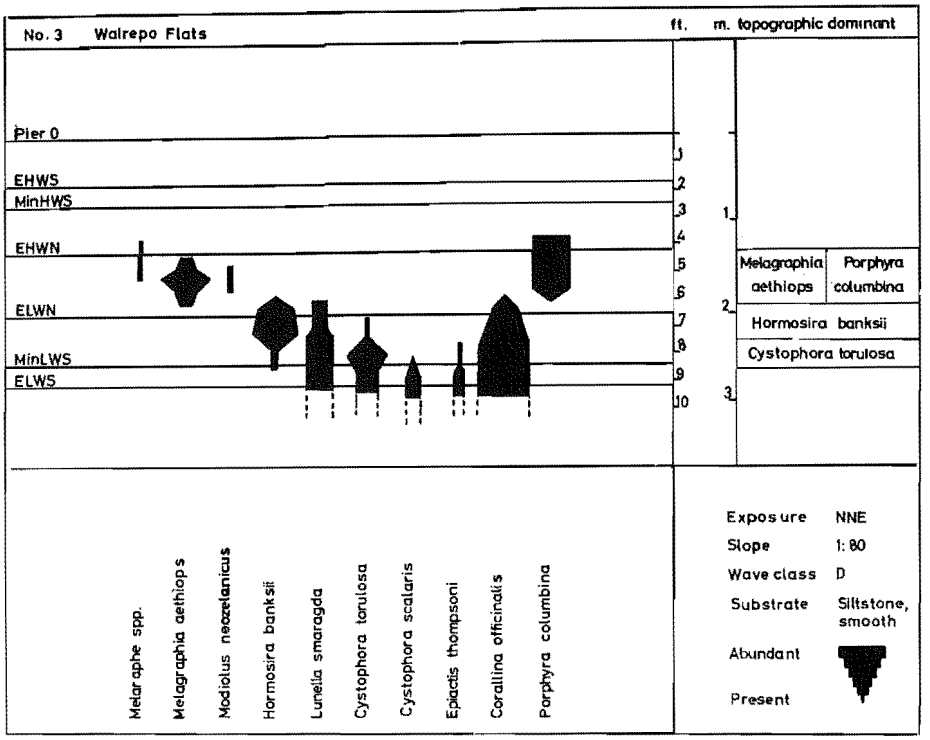

No. 2 Avoco Point
ft.
m. topographic dominant
Pier 0
EHWS
MinHWS
EHWN
ELWN
MinLWS
ELWS
1
2
3
4
5
6
7
8
9
10
1
2
3
Melaraphe oliveri
Melagraphia aethiops
Cellana spp.
algal turf
Melaraphe oliveri
Melaraphe cincta
Melagraphia aethiops
Hormosira banksii
Cellana spp.
Chamaesipho columna
Lunella smaragda
algal turf
Cystophora spp.
Carpophyllum maschalocarpum
Corallina officinalis
Porphyra columbina
Exposure NE
Slope 1.5 overall
Wave class C
Substrate Limestone, angled
Abundant
Present

Figure 8.

Vertical distribution and abundance of the organisms recorded on transect No. 1, at Laboratory Rocks.

Figure 9.

Vertical distribution and abundance of the organisms recorded on transect No. 2, at Avoca Point.


No. 3 Walrepo Flats
ft.
m.
topographic dominant
Pier 0
EHWS
MinHWS
EHWN
ELWN
MinLWS
ELWS
1
2
3
Melagraphia aethiops
Porphyra columbina
Hormosira banksii
Cystophora torulosa
Melaraphe spp.
Melagraphia aethiops
Modiolus neozelanicus
Hormosira banksii
Lunella smaragda
Cystophora torulosa
Cystophora scalaris
Epiactis thompsoni
Corallina officinalis
Porphyra columbina
Exposure NNE
Slope 1:80
Wave class D
Substrate Siltstone, smooth
Abundant
Present

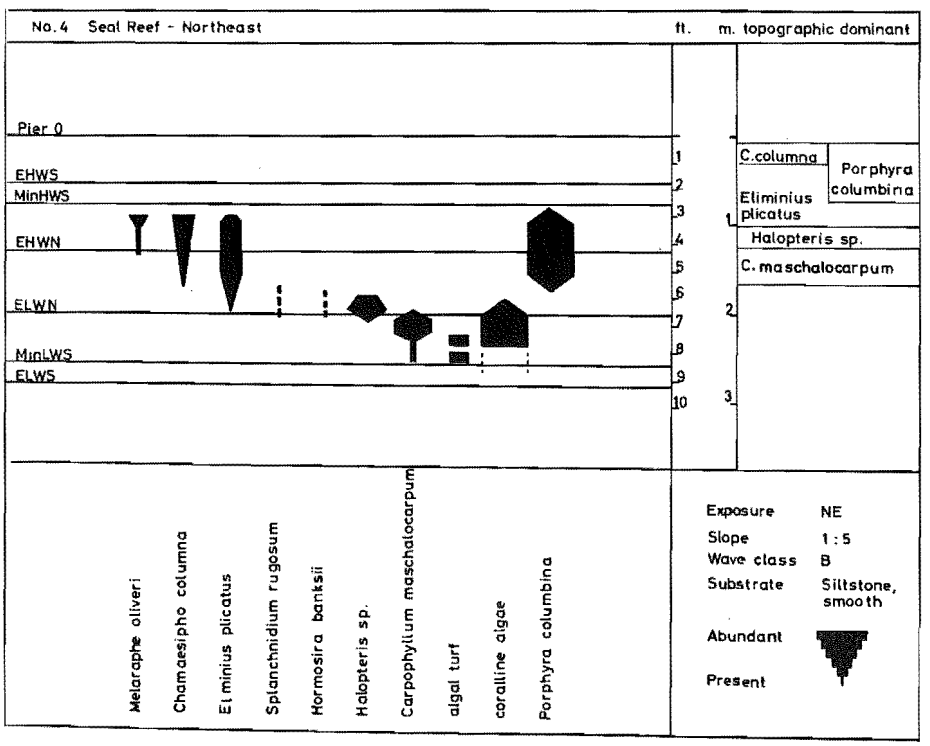
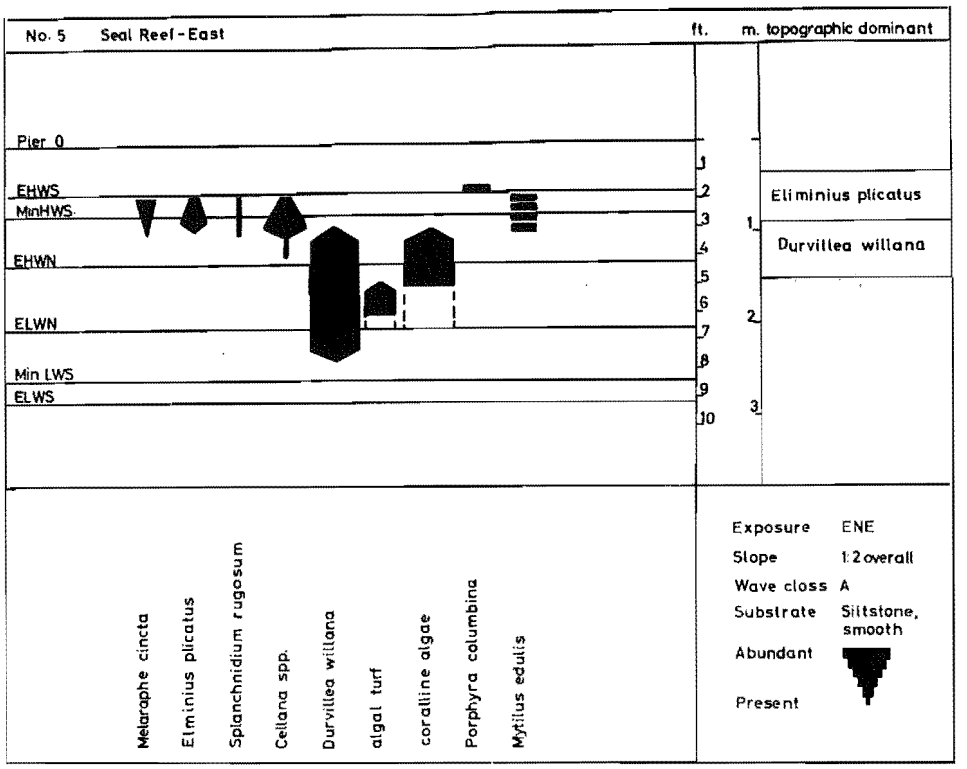

No. 4 Seal Reef - Northeast
ft.
m.
topographic dominant
Pier 0
EHWS
MinHWS
EHWN
ELWN
MinLWS
ELWS
1
2
3
C.columna
Porphyra columbina
Eliminius plicatus
Halopteris sp.
C. maschalocarpum
Melaraphe oliveri
Chamaesipho columna
Eliminius plicatus
Splanchnidium rugosum
Hormosira banksii
Halopteris sp.
Carpophyllum maschalocarpum
algal turf
coralline algae
Porphyra columbina
Exposure NE
Slope 1:5
Wave class B
Substrate Siltstone, smooth
Abundant
Present

Figure 10.

The vertical distribution and abundance of the organisms recorded on transect No. 3, at Wairepo Flats.

Figure 11.

The vertical distribution and abundance of the organisms recorded on transect No. 4, at Seal Reef - Northeast.


No. 5 Seal Reef - East
ft.
m.
topographic dominant
Pier 0
EHWS
MinHWS
EHWN
ELWN
Min LWS
ELWS
1
2
3
4
5
6
7
8
9
10
1
2
3
Eliminius plicatus
Durvillea willana
Melaraphe cincta
Elminius plicatus
Splanchnidium rugosum
Cellana spp.
Durvillea willana
algal turf
coralline algae
Porphyra columbina
Mytilus edulis
Exposure ENE
Slope 1:2 overall
Wave class A
Substrate Siltstone, smooth
Abundant
Present

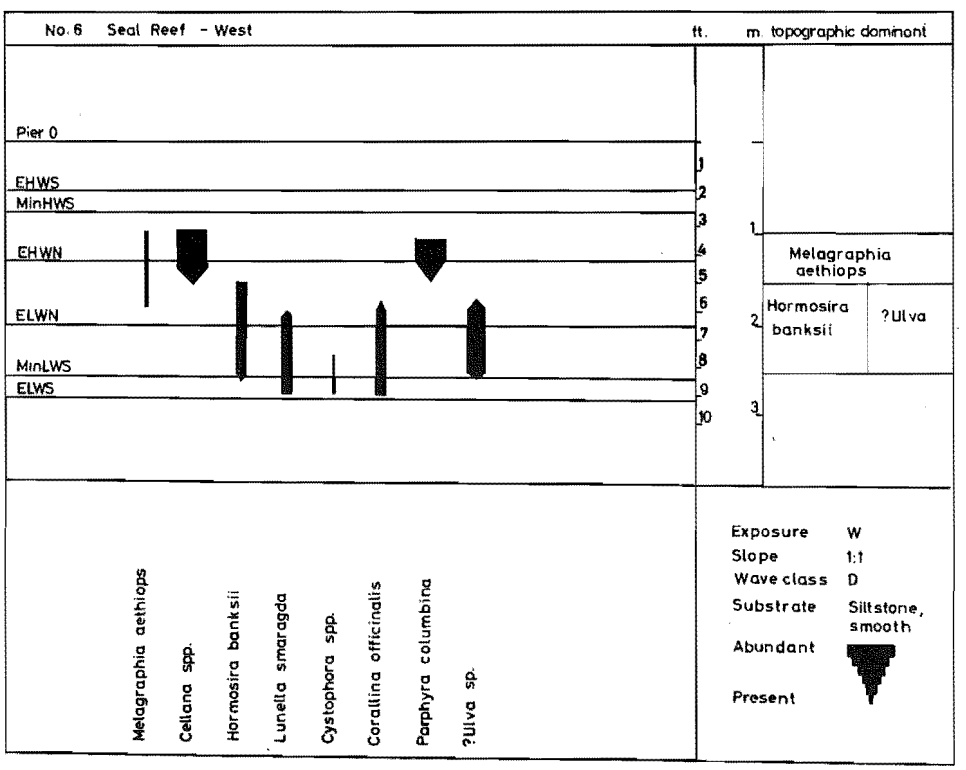
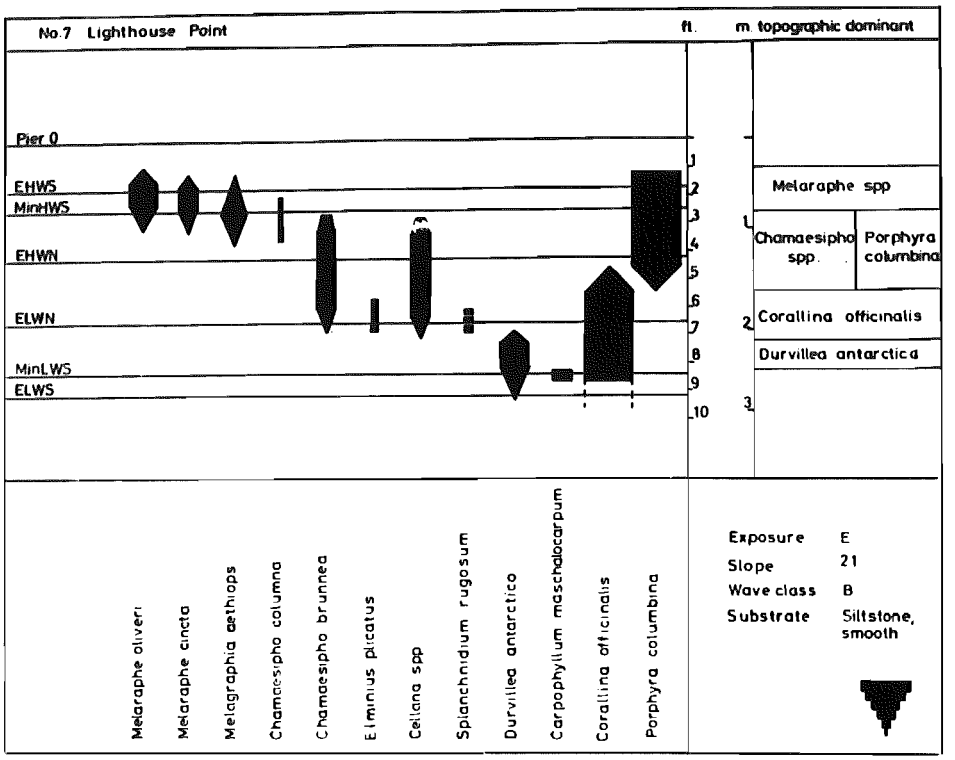

No. 6 Seal Reef - West
ft.
m.
topographic dominant
Pier 0
EHWS
MinHWS
EHWN
ELWN
MinLWS
ELWS
1
2
3
4
5
6
7
8
9
10
1
2
3
Melagraphia aethiops
Hormosira banksii
?Ulva
Melagraphia aethiops
Cellana spp.
Hormosira banksii
Lunella smaragda
Cystophora spp.
Corallina officinalis
Porphyra columbina
?Ulva sp.
Exposure W
Slope 1:1
Wave class D
Substrate Siltstone, smooth
Abundant
Present

Figure 12.

The vertical distribution and abundance of the organisms recorded on transect No. 5, at Seal Reef - East.

Figure 13.

The vertical distribution and abundance of the organisms recorded on transect No. 6, at Seal Reef - West.


No.7 Lighthouse Point
ft.
m
topographic dominant
Pier 0
EHWS
MinHWS
EHWN
ELWN
MinLWS
ELWS
1
2
3
4
5
6
7
8
9
10
1
2
3
Melaraphe spp
Chamaesipho spp.
Porphyra columbina
Corallina officinalis
Durvillea antarctica
Melaraphe oliveri
Melaraphe cincta
Melagraphia aethiops
Chamaesipho columna
Chamaesipho brunnea
Elminius plicatus
Cellana spp
Splanchnidium rugosum
Durvillea antarctica
Carpophyllum maschalocarpum
Corallina officinalis
Porphyra columbina
Exposure E
Slope 21
Wave class B
Substrate Siltstone, smooth

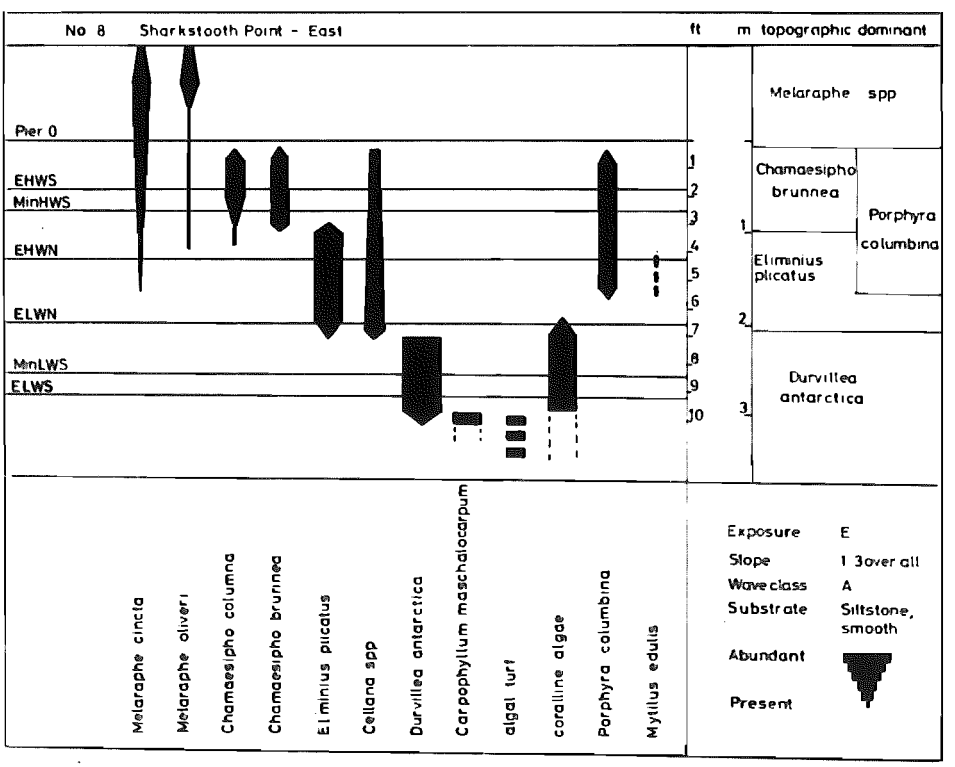
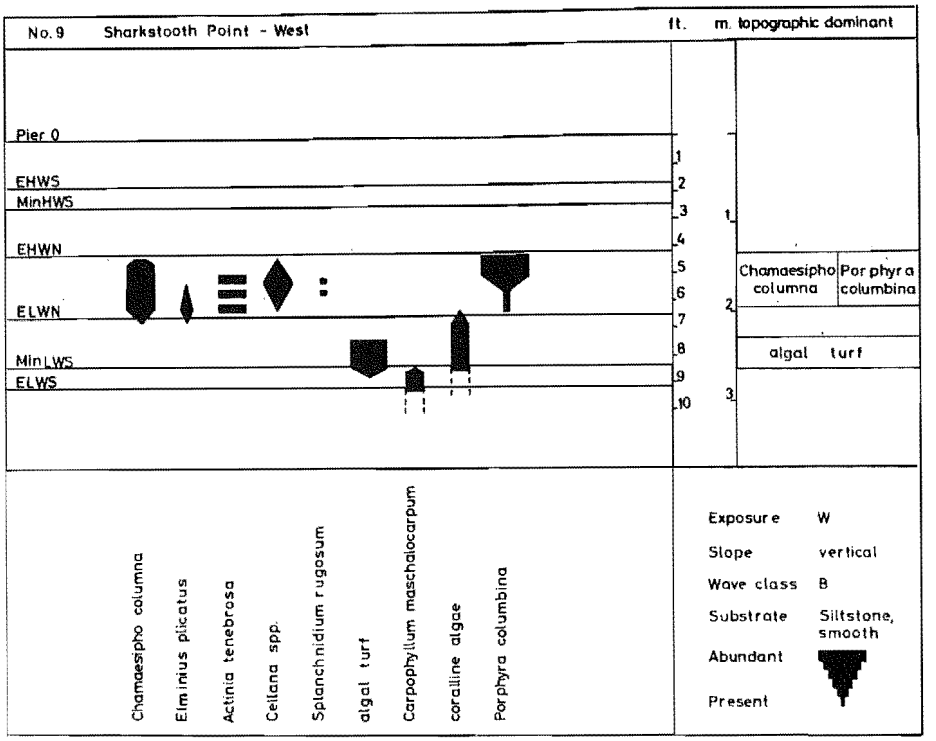

No 8 Sharkstooth Point - East
ft
m
topographic dominant
Pier 0
EHWS
MinHWS
EHWN
ELWN
MinLWS
ELWS
1
2
3
4
5
6
7
8
9
10
1
2
3
Melaraphe spp
Chamaesipho brunnea
Porphyra columbina
Elminius plicatus
Durvillea antarctica
Melaraphe cincta
Melaraphe oliveri
Chamaesipho columna
Chamaesipho brunnea
Elminius plicatus
Cellana spp
Durvillea antarctica
Carpophyllum maschalocarpum
algal turf
coralline algae
Porphyra columbina
Mytilus edulis
Exposure E
Slope 1 3over all
Wave class A
Substrate Siltstone, smooth
Abundant
Present

Figure 14.

The vertical distribution and abundance of the organisms recorded on transect No. 7, at Lighthouse Point.

Figure 15.

The vertical distribution and abundance of the organisms recorded on transect No. 8, at Sharkstooth Point - East.


No. 9 Sharkstooth Point - West
ft.
m.
topographic dominant
Pier 0
EHWS
MinHWS
EHWN
ELWN
MinLWS
ELWS
1
2
3
4
5
6
7
8
9
10
1
2
3
Chamaesipho columna
Porphyra columbina
algal turf
Chamaesipho columna
Elminius plicatus
Actinia tenebrosa
Cellana spp.
Splanchnidium rugosum
algal turf
Carpophyllum maschalocarpum
coralline algae
Porphyra columbina
Exposure W
Slope vertical
Wave class B
Substrate Siltstone, smooth
Abundant
Present

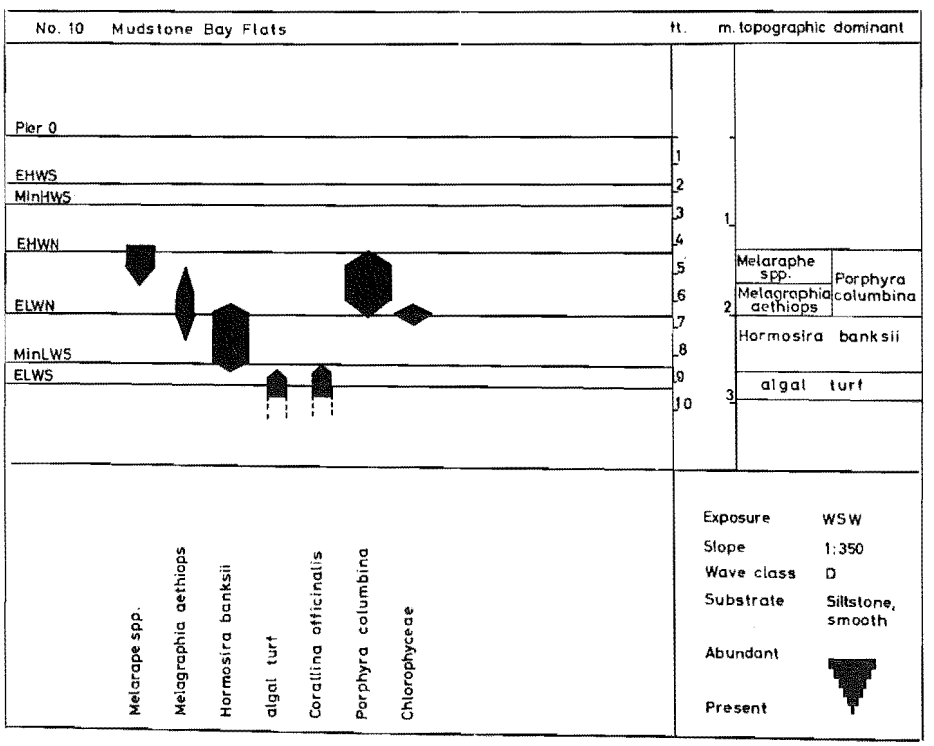
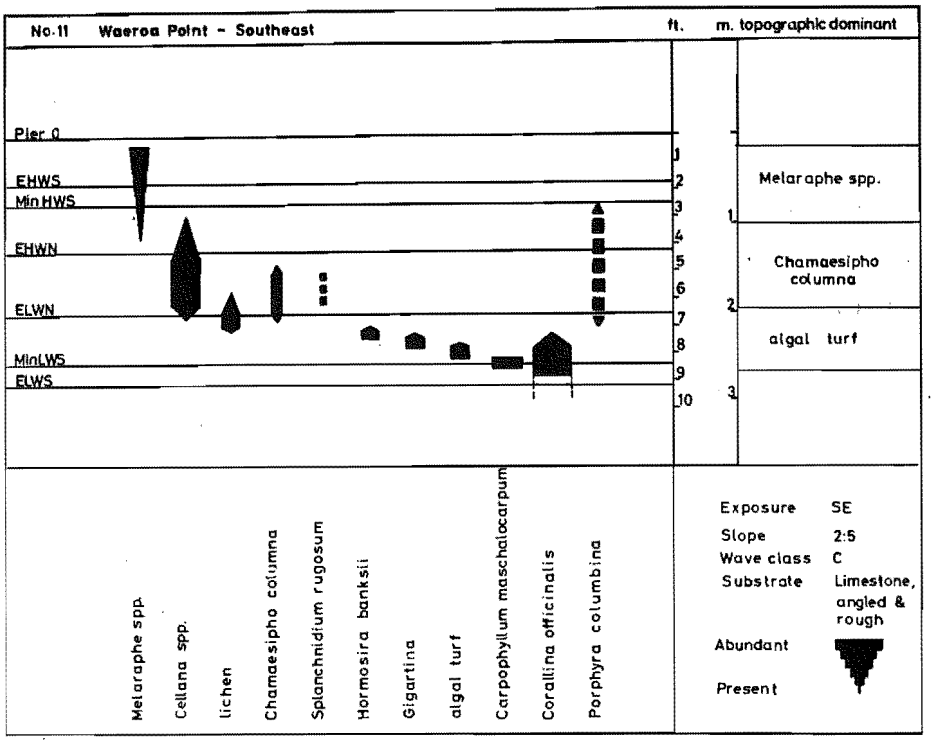

No. 10 Mudstone Bay Flats
ft.
m.
topographic dominant
Pier 0
EHWS
MinHWS
EHWN
ELWN
MinLWS
ELWS
1
2
3
4
5
6
7
8
9
10
1
2
3
Melaraphe spp.
Porphyra columbina
Melagraphia aethiops
Hormosira banksii
algal turf
Melarape spp.
Melagraphia aethiops
Hormosira banksii
algal turf
Corallina officinalis
Porphyra columbina
Chlorophyceae
Exposure WSW
Slope 1:350
Wave class D
Substrate Siltstone, smooth
Abundant
Present

Figure 16.

The vertical distribution and abundance of the organisms recorded on transect No. 9, at Sharkstooth Point - West.

Figure 17.

The vertical distribution and abundance of the organisms recorded on transect No. 10, at Mudstone Bay Flats.


No.11 Waeroa Point - Southeast
ft.
m. topographic dominant
Pier 0
EHWS
MinHWS
EHWN
ELWN
MinLWS
ELWS
1
2
3
4
5
6
7
8
9
10
1
2
3
Melaraphe spp.
Chamaesipho columna
algal turf
Melaraphe spp.
Cellana spp.
lichen
Chamaesipho columna
Splanchnidium rugosum
Hormosira banksii
Gigartina
algal turf
Carpophyllum maschalocarpum
Corallina officinalis
Porphyra columbina
Exposure SE
Slope 2:5
Wave class C
Substrate Limestone, angled & rough
Abundant
Present

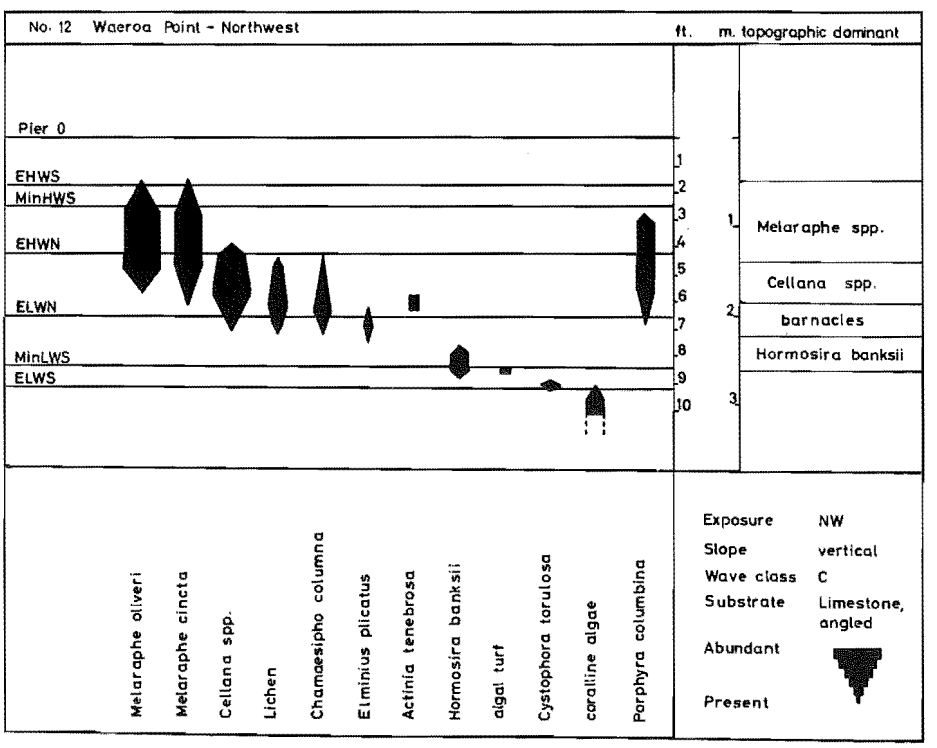

No. 12 Waeroa Point - Northwest
ft.
m. topographic dominant
Pier 0
EHWS
MinHWS
EHWN
ELWN
MinLWS
ELWS
1
2
3
4
5
6
7
8
9
10
1
2
3
Melaraphe spp.
Cellana spp.
barnacles
Hormosira banksii
Melaraphe oliveri
Melaraphe cincta
Cellana spp.
Lichen
Chamaesipho columna
Elminius plicatus
Actinia tenebrosa
Hormosira banksii
algal turf
Cystophora torulosa
coralline algae
Porphyra columbina
Exposure NW
Slope vertical
Wave class C
Substrate Limestone, angled
Abundant
Present

Figure 18.

The vertical distribution and abundance of the organisms recorded on transect No. 11, at Waeroa Point - Southeast.

Figure 19.

The vertical distribution and abundance of the organisms recorded on transect No. 12, at Waeroa Point - Northwest.

Seasonal changes

The rotation of the seasons brings many changes to the seashore. These changes are seldom as obvious as those of the terrestrial habitat. This may be due to the tempering effect of the sea mass or, as is more likely, due to their being generally unobserved.

The seasonal changes may be categorized as: the presence or absence of various phases of the life-cycle of certain organisms, differences in size, growth rate, or appearance of organisms, and changes in the distributions of organisms.

The most obvious seasonal variations occur in the first category. Porphyra columbina, by analogy with other members of the genus, is assumed to have an alternation of forms: a macroscopic lithophytic form, and a microscopic Conchocoelis-stage, that bores into molluscan shells. In April and May the macroscopic form begins to be obvious on the higher intertidal rocks and on the shells of browzing molluscs. By June, the rock platforms from EHWN to the top of the H. banksii band have a heavy cover of P. columbina. Where the H. banksii band is absent, the lower edge of the P. columbina band very nearly coincides with the top of the Corallina officinalis band.

In a similar manner, the alternation of forms common among the red algae explains other changes. These changes include the periodic increase of Asparagopsis armata in the shallow waters of the sheltered bays. The alternate form, Falkenbergia rufalancsa, is considerably less obvious. Fluctations in the composition of the algal turf may be explained in this way, as well.

Less easily explained are the seasonal variations in the brown algae. For seven months, from April to November, the C. officinalis beds of the sheltered bays and channels have a heavy growth of Colpomenia sinuosa, a yellow-brown parchment-like sac. Then, in November, one notices that the yellow-brown saccate epiphyte on the C. officinalis is no longer C. sinuosa, but Leathesia difformis, a heavy walled form with a similar habit and habitat. Another saccate brown alga makes an appearance in the same areas, Adenocystis utricularis. It appears suddenly in late October or early November, shows signs of desiccation in March or April and is suddenly gone. Where, and in what form, do these species exist when they are not in evidence on the rocks?

Other seasonal appearances and disappearances are indicated on figure 40 where some comparisons are made with other reports from New Zealand shores. These records were abstracted from settlement surveys made on both coasts of the North Island (Luckens 1964) and from the diary observations made at Kaikoura. The northern observations were included as they were of species that occur at Kaikoura and often represented species for which there were no seasonal records at Kaikoura. Where complimentary records did exist, it appeared that the settlement season in the north was initiated earlier and continued longer, as a rule.

Two aspects of seasonal change are evident in the shift of distributions. One is a vertical shift, particularly of upper limits. The other is an apparent change in habits, most noticeable in the mobile species. The "Cat's Eye", Lunella smaragda, typifies both.

During the winter months, L. smaragda extends its upper limit; sheltering under the growth of P. columbina on the sheltered platforms or coming up into the algal turf in the moderately exposed situations. On the platforms no evident change in behavior is noted. But, in very exposed situations, L. smaragda does not normally leave the sublittoral. When it does, it is quite conspicuous in the algal turf. Individuals have been observed in this situation for periods of several days. At each low tide they are in the same position and show no signs of having moved. This is a different behavior pattern from that observed in the summer when attempts to observe the behavior of L. smaragda in the field were frustrated by the extreme mobility of the animal.

A similar excursion from sublittoral situations and hidden places in the littoral is made by Benhamina obliquata. Late in November and early in December B. obliquata appears briefly in the littoral and lays down its "onion ring" egg masses.

Several algae show fluctuations of upper limits during the year. Some are very slight. H. banksii raises its upper limit in the early spring and early autumn by an extensive growth of new plants. These die back some weeks later to restore the old limits. Various constituents of the algal turf, notably the Echinothamnion spp. and Halopteris spp. have slight shifts in range.

A greater shift is made by the prostrate form of C. officinalis on the exposed shores. Here the "pink paint" layer of C. officinalis extends considerably its upper range, only to die back to a thin white crust in the summer. This has all the appearances of a desiccation effect.

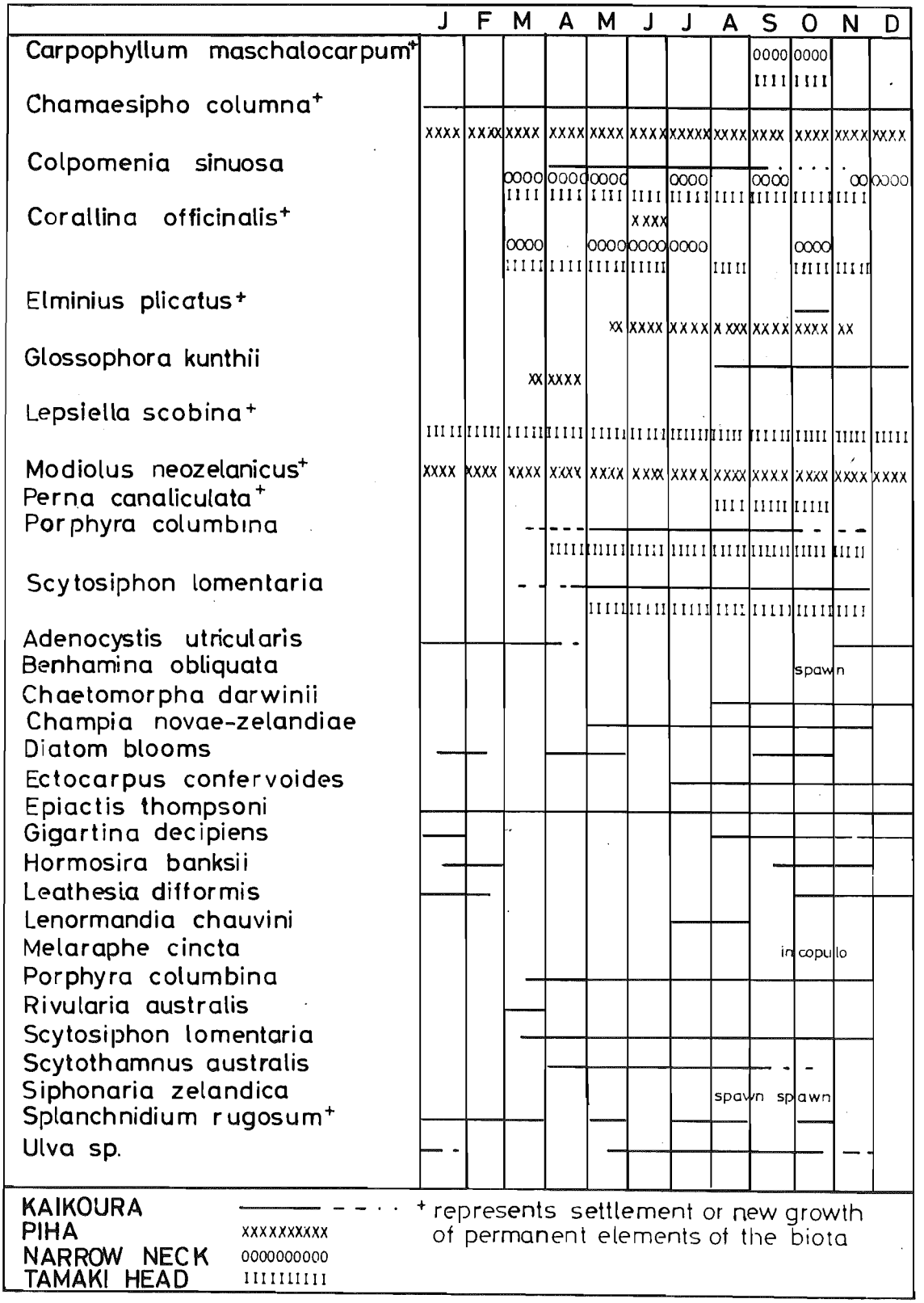

J F M A M J J A S O N D
Carpophyllum maschalocarpum+
Chamaesipho columna+
Colpomenia sinuosa
Corallina officinalis+
Elminius plicatus+
Glossophora kunthii
Lepsiella scobina+
Modiolus neozelanicus+
Perna canaliculata+
Porphyra columbina
Scytosiphon lomentaria
Adenocystis utricularis
Benhamina obliquata
Chaetomorpha darwinii
Champia novae-zelandiae
Diatom blooms
Ectocarpus confervoides
Epiactis thompsoni
Gigartina decipiens
Hormosira banksii
Leathesia difformis
Lenormandia chauvini
Melaraphe cincta
Porphyra columbina
Rivularia australis
Scytosiphon lomentaria
Scytothamnus australis
Siphonaria zelandica
Splanchnidium rugosum+
Ulva sp.
spawn
in copulo
spawn spawn
KAIKOURA
PIHA
NARROW NECK
TAMAKI HEAD
+ represents settlement or new growth of permanent elements of the biota

Figure 40.

A list of organisms found on the shores of the Kaikoura Peninsula giving the times of occurrence, or settlement, extracted from field notes at Kaikoura and from Luckens (1964). Piha, Narrow Neck and Tamaki Head are on the North Island and allowance must be made for the climatic difference inherent in the difference in latitude and for the temperature differences due to off-shore currents. It would be expected that summer species would occur sooner, and last longer on the North Island and conversely that winter species would occur sooner and stay longer at Kaikoura.

Discussion

Fitting specific cases to general principles always presents difficulties and so it is with the zonation pattern of the Kaikoura Peninsula. The interpertation of an organism's role in a scheme, such as that proposed by Lewis (1964), requires a knowledge of the organisms distribution throughout its geographical range. Without this knowledge one can easily accept the anomaly for the usual for, without comparative information, there are no anomalies. For further information on distributions along this coast we have the papers of Knox (1953, 1960) and Batham (1956, 1958).

At Kaikoura there are very few problems attached to applying Lewis's scheme to the littoral fringe or the upper half of the eulittoral zone. The upper limit of the littoral fringe seldom exists, except as the upper limit of the rocky shore environment, because of the shingle bank that lies on top of the rock platforms. The littoral fringe/eulittoral zone boundary is definable as the bottom of the unmixed littorinid (Melaraphe spp.) population or, more properly, the top limit of the barnacle population or other species population that extends highest into the littorinid population. At Kaikoura, the major barnacle species are: Chamaesipho brunnea, C. columna, and Elminius plicatus. The proportion of any particular species on the shore depends largely upon the degree of wave exposure. C. columna is found unmixed where the wave action is light. As the wave action increases C. brunnea and E. plicatus are to be found mixed with the C. columna. When the wave action becomes heavy, corresponding with that found in the (B) zone

(cf. I. B. 2.) the proportion of C. brunnea begins to drop so that in the (A) zone only E. plicatus and C. columna are found, with E. plicatus being predominant. At the most exposed points an unmixed E. plicatus belt is found. In the very sheltered areas, where the barnacles are absent, the trochid Melagraphia aethiops becomes the indicator organism.

Through the eulittoral, the patterns are fairly distinct. Molluscan banding is obvious. On sheltered shores the series is Melaraphe/M. aethiops, M. aethiops/L. smaragda. When wave action becomes more servere, the pattern shifts to Melaraphe spp./Cellana spp., Cellana spp., Cellana spp./Patelloida corticata Siphonaria novae-zelandiae.

Algal banding in the sheltered areas begins at approximately the mid-tide level with thick carpets of Hormosira banksii. Below the H. banksii are the Cystophora spp. This pattern is replaced by one of Rhodophyceaen turf above Carpophyllum maschalocarpum, as the exposure increases. At maximum exposures, both belts are replaced by Durvillea spp.

Two other algal species must be considered in a description of the general zonation pattern. In winter, Porphyra columbina may cover nearly all rock surface from the effective neap high tide wetting-level down to the upper levels of the permanent algal population. Corallina officinalis comes up from the sublittoral as an undergrowth of the algal belts in sheltered areas and as a band former in its own right on the more exposed shores.

The main problem in applying the Lewis scheme, or almost any of the other "universal" schemes, is to determine the boundary between eulittoral and sublittoral.

Lewis recognized this difficulty by calling this division an "over-simplification". He recognizes the upper limit of the laminarians as the upper limit of the sublittoral. However, at Kaikoura there are no good, clean, sharp, laminarian borders. In fact, laminarians are not particularly abundant about the peninsula. There are patches of Lessonia variegata and Ecklonia radiata and occasional bands of Marginariella boryana. Only the M. boryana is universal enough and forms discrete enough bands to serve as an indicator.

Without further knowledge of distribution patterns on other shores of the South Island, one might easily assign a sublittoral fringe label to the areas dominated by Cystophora spp. C. maschalocarpum, and possibly Durvillea spp. However, reference to Knox (1953, 1960 and pers. comm.) indicates that a Lessonia band is a common feature on many of these shores, whereas L. variegata has only a patchy distribution on the peninsula. It is evident that the Lessonia band, where present, is the best marker of the upper sublittoral and that Cystophora spp., C. maschalocarpum, and Durvillea spp. lie above the Lessonia and are therefore truly littoral species.

In the absence of a definite sublittoral population, at the appropriate levels, a number of littoral organisms extend their range to levels seldom exposed to air.

Other organisms, of the sublittoral, extend their range well into the littoral, e.g., L. smaragda.

Still others normally have a distribution that straddles the sublittoral/littoral boundary as does C. officinalis.

It is concluded that the sublittoral/littoral boundary is seldom discrete, at Kaikoura, and that often the littoral

distributions extend lower than might be expected by experience of other shores. Where the boundary can be sharply distinguished, it may be marked as the upper limits of M. boryana, L. variegata, or by reference to some of the less conspicuous flora and fauna, e.g., Haliotis iris, Perna canalicula, or Arthrocardia sp.

The biogeographic position of the Kaikoura coast.

To interpret and understand the results of this local survey, it is necessary to consider the entire pattern of intertidal species distribution on the coasts of New Zealand and other related coasts. This will enable us to determine if the distributions on the Kaikoura Peninsula fit the over-all pattern, if it is in any way anomalous, and if the geographic location helps to explain the local situation. Conversely, the Kaikoura survey will expand our current knowledge of the distributions of the rocky shore species of the coasts of New Zealand.

To date, the detailed locality surveys of New Zealand coasts have been largely limited to the east coast. Surveys are available for the Hauraki Gulf (Dellow 1955), islands in the Hauraki Gulf (Berquist 1960a), Rangitoto Island (Carnahan 1952), Stanmore Bay (Chapman 1950), the Poor Knights Islands (Cranwell and Moore 1938), the Northland shores (Berquist 1960b), Banks Peninsula (Knox 1953), and the Otago Peninsula (Batham 1956, 1958). General accounts of the ecology of the coasts of New Zealand have been written by Oliver (1923) and Knox (1960). There are also several papers concerning the distributions of specific taxonomic groups, prominent

among these are: Fell (1949) echinoderms, Moore (1961) seaweeds, and Powell (1940, 1961b) molluscs.

Information concerning distribution patterns on the west coast of New Zealand are few (Beveridge and Chapman 1950) (Batham 1965) (Luckens 1964). From the general accounts of Knox (1960, 1963a) and Moore (1961) it can be seen that there are differences between the east and west coast that may prove to be very significant when they are more fully documented. Because of the lack of documentation, following references to the coasts of New Zealand should be understood to apply only to the eastern coast.

The biogeography of the New Zealand and Australian coasts has been reviewed and analyzed recently by Knox (1960, 1963a, 1963b). In these analyses, two systems of classifying the distribution of intertidal organisms on the east coast of New Zealand were discussed. The first system recognizes ten distribution patterns based upon the distributional ranges of a large number of intertidal dominants. Four of these patterns extend from Stewart Island northward: the first extending only as far as Dunedin, the second to Cook Strait, the third to Castlepoint, the fourth to East Cape. Five patterns extend from Cape Reinga southward: One extends only to

East Cape, the second to the Mahia Peninsula, the third to Castlepoint, a fourth to Cook Strait, and a fifth to the vicinity of Kaikoura. The tenth pattern is described as an universal element extending from Cape Reinga to Stewart Island. From these ten patterns, the following five categories were extracted:

(1) extreme southern species.

(2) southern species not extending north of East Cape.

(3) extreme northern species.

(4) northern species not extending south of Kaikoura.

(5) an universal component.

From these categories, the presence of a southern centre of distribution and a northern centre of distribution were postulated. This led Knox to consider the second method of classifying the distribution of coastal species, by the definition of biogeographic provinces. New Zealand coastal provinces were first proposed by Finlay (1925, 1926) for the interpretation of the distribution of molluscan species. As such, the provinces have been much discussed and modified in the literature (Powell 1937, 1940, 1951, 1955, 1961a) (Fleming 1944) (Dell 1962). Similar divisions have been proposed upon the basis of echinoderm distribution (Fell 1949, 1953) (Pawson

1961), and the distribution of algal species (Moore 1947, 1961). Knox (1963a), on the basis of these interpretations and his own analysis of the distribution of intertidal dominants, recognized the following provincial areas:

Forsterian - Stewart Island and the Otago coast to a point north of Dunedin.

Cookian - From the northern boundary of the Forsterian to East Cape.

Aupourian - From East Cape to Cape Reinga.

The Forsterian and Aupourian provinces were considered to be centres of distribution and the Cookian was interpreted as an area of overlap.

The Kaikoura Peninsula lies near the centre of the Cookian province, as described above. It is an area of considerable interest in that only one other shore of the Cookian province, Taylor's Mistake on the Banks Peninsula, has been surveyed in detail (Knox 1953), and because five of the distribution patterns, upon which Knox based his conclusions, extend past this point. Three are southern distributions, one is northern, and the fifth is the universal element. Another northern element reaches the southern shore of Cook Strait which is a short distance to the north of the peninsula.

As might be expected of any specific locality, certain features of the intertidal species distribution, at Kaikoura, vary from the generalized pattern outlined for the east coast of the Cookian province by Knox.

The densities of all mussel species are low. There are two small beds of Modiolus neozelanicus on the peninsula. These small mussels are a prominent feature of the upper littoral in all three provinces.

Perna canaliculus is present in small numbers in the lower littoral of the more exposed portions of Sharkstooth Point and Seal Reef. There seems to be some confusion in the literature concerning the distribution of this mussel. Knox (1960) lists P. canaliculus as an indicator organism of the lower littoral of the Forsterian province and specifically treats of it in his description of Taylor's Mistake in the Cookian province. Yet, Powell (1961b) calls it the "North Island mussel" and Knox (1963a) refers to it as a "northern mussel" of the Cookian and Aupourian provinces and specifies its absence from the Forsterian.

Mytilus edulis aoteanus, a band former both to the north and the south, is found scattered about the peninsula in areas of moderate exposure. Even less prominent is the ribbed mussel, Aulacomya maoriana, a

band former to the south.

Among gastropod species listed as characteristic of the Cookian province, the following are absent or rare on the Kaikoura Peninsula: Neothais scalaris, Lepsithais lacunosus, and Zediloma digna. These absences may be due to habitat preferences. Z. digna is found in quantity at the boulder beaches south of the mouth of the Kahutara River, only a few miles from the peninsula.

Other species commonly found within a few miles of the peninsula, but rarely on the peninsula, are: Cellana strigilis, a southern limpet, Gigartina apoda, G. decipiens, and G. angulata, abundant red algae of the lower littoral and upper sublittoral from the Kahutara River to Haumuri Bluffs.

Among the algae listed as characteristic of the Cookian province, Xiphophora chondrophylla is notable for its absence from Haumuri Bluffs, Kaikoura, and Cape Campbell. Ilea fascia and Myriogloea lindaueri, both seasonal forms, are rare on the peninsula but are found at points north and south. Mentioned in an earlier section were the low concentrations of the laminarians, Ecklonia radiata and Lessonia variegata.

Though the boundaries for the provinces have been

placed at different points by different authors, according to the taxonomic group considered, or the amount of data available, the concept of a northern and a southern distribution centre with an area of overlap is common to all the analyses. To determine how the Kaikoura Peninsula figures in this region of overlap, the species of red algae, brown algae, and the molluscs listed for the Kaikoura Peninsula in this paper were compared with the previously known extent of their ranges. These three groups were chosen because of their prominence in the species list and because the comparative information was readily available. Algal comparisons were made with the list of Dellow (1955) for the Hauraki Gulf, which is distinctly within the northern centre of distribution, and the list of Naylor (1954) for the Dunedin area and Otago coast, comprising the South Island portion of the southern distribution centre. Molluscan distributions were taken from Powell (1961b). Of the sixty-three species of red algae, eighteen were found to be members of the universal component (Antithamnion applicatum, Bostrychia arbuscula, Centroceras clavulatum, Ceramium uncinatum, Champia novae-zelandiae, Cladyhymenia oblongifolia, Corallina officinalis, Craspedocarpus erosus, Euzoniella incisa,

Falkenbergia rufolanosa, Gelidium caulacantheum, Gymnogongrus nodiferus, Jania rubens, Melanthalia abscissa, Pleonosporium hirtum, Plocamium angustum, Porphyra columbina, Porphyra subtumens). Four were on the northern list but not the southern list (Abroteia suborbiculata, Gigartina atropurpurea, Plocamium abnorme, Pterocladia lucida). Twenty-seven were on the southern list but not the northern (Ballia scoparia, Callophyllis calliblepharoides, Curdiae coriaceae, Echinothamnion hookeri, E. lyallii, E. mallardiae, Epymenia wilsonis, Euptilota formossissma, Gigartina apoda, G. decipiens, G. longifolia, Grateloupia intestinalis, Griffithsia antarctica, Hymenena palmata, Hymenocladia lanceolata, Laingia hookeri, Lenormandia chauvinii, Myriogramme multinervis, Plocamium brachiocarpum, P. costatum, Polysiphonia infestans, Rhodophyllis gunnii, Schizymenia novae-zelandiae, Streblocladia neglecta, Trematocarpus acicularis, Warrenia comosa). The remaining species were not included in either list. Of the thirty-five species of brown algae, nineteen were included in both the northern and southern lists (Carpophyllum maschalocarpum, Colpomenia sinuosa, Cystophora retroflexa, C. torulosa,

Durvillea antarctica, Ecklonia radiata, Ectocarpus confervoides, Glossophora kunthii, Halopteris spicigera, Hormosira banksii, Leathesia difformis, Lessonia variegata, Myriogloea lindaueri, Notheia anomala, Ralfsia verrucosa, Sargassum sinclairii, Scytosiphon lomentaria, Scytothamnus australis, Splachnidium rugosum). Five were found on the northern list but not on the southern list (Carpomitra costata, Dictyota ocellata, Haplospongidium saxigenum, Landsburgia quercifolia, Tinocladia novae-zelandiae). Eleven were found on the southern list but not on the northern list (Adenocystis utricularis, Corynophloaea cystophorae, Cystophora scalaris, Desmerestia firma, Durvillea willana, Macrocystis pyrifera, Marginariella boryana, M. urvilliana, Microzonia velutina, Papenfussiella lutea, Scytothamnus fasciculatus).

Of the seventy-three molluscan species, forty-eight were recorded for all three provinces (Amaurochiton glaucus, Eudoxochiton nobilis, Ischnochiton maorianus, Onithochiton neglectus, Sypharochiton pelliserpentis, S. sinclairi, Atalacmea fragilis, Cantharidus opalus, Cellana ornata, C. radians, Emarginula striatula, Haliotis australis, H. iris, Haurakia hamiltoni, Haustrum haustorium, Lepsiella albomarginata, Leuconopsis

obsoleta, Liotella polypleura, Lunella smaragda, Maoricrypta monxyla, Melagraphia aethiops, Melaraphe cincta, M. oliveri, Notoacmea daedala, N. parvaconoides, Notoacmea scopulina, Patelloida corticata, Risselopsis varia, Scrobs hedleyi, Scutus breviculus, Sigapatella novae-zelandiae, Trochus tiaratus, Zeacumantus subcarinatus, Zediloma atrovirens, Z. digna, Zemitrella choana, Aglaja cylindrica, Siphonaria novae-zelandiae, Modiolaria barbata, Modiolus neozelanicus, Mytilus edulis, Notcorbula zelandica, Pachykellia minima, Perna canaliculus, Zelithophaga truncatus, Zemyllita stowei, Octopus maorum, Robsonella australis). Ten species were listed for the Aupourian and Cookian provinces but not the Forsterian (Acanthochiton zelandicus, Cellana denticulata, Cominella adspersa, C. maculosa, Herpetopoma bella, Lepsiella scobina, Merelina lyalliana, Aeolidia gracilis, Pleurobranchiae novae-zelandiae, Onchidella flavescens). Nine species were listed for the Forsterian and Cookian provinces but not for the Aupourian (Frembleya egregia, Cellana flava, C. strigilis, Estea rekohuana, Haliotis virginea, Skenella pfefferi, Benhamina obliquata, Aulacomya maoriana, Lasea hinemoa). The remainder were largely manuscript species of Mr. Winston Ponder (pers. comm.) with unknown distributions.

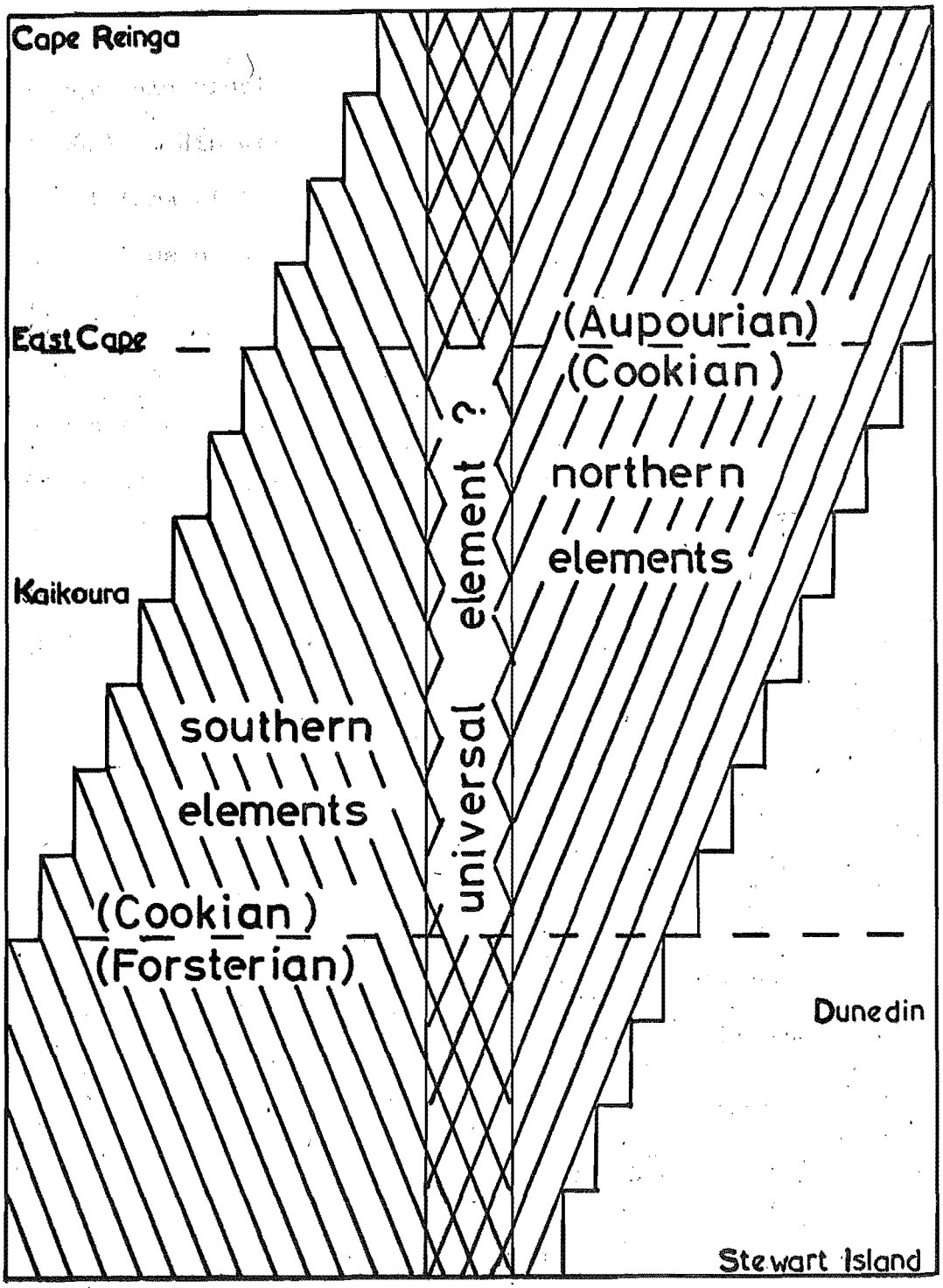
It is indicated by the above that the Kaikoura Peninsula does lie in an area of overlapping northern and southern distributions. It is also evident that the universal element is the predominant one and that the northern and southern elements are well balanced with only a slightly higher incidence of southern species.

As the previous accounts of the east coast of the Cookian province are based upon one detailed locality survey and isolated distribution records for specific taxa, it seems likely that the discontinuous distribution patterns detailed by Knox (1960, 1963a) may reflect only discontinuities in sampling. It may well be that more complete distributional records of a larger number of species will show a more continuous range of distributional end-points, with the breaks occurring at each substrate barrier. In the case of rocky intertidal organisms, this would mean that every major rocky shore could represent the northern and/or southern limit of distribution for some species. This postulated situation is diagrammatically represented on Figure 60. A paper by Pawson (1965) shows just such a pattern of distributions for stenobathic shelf echinoderms.

The concept of dividing New Zealand coasts into bio-

Figure 60

A diagrammatic representation of the postulated distribution patterns of intertidal species on the eastern coast of New Zealand. Each bar represents the range of a species, or group of species, and terminates at a major habitat barrier.


Cape Reinga
East Cape
Kaikoura
Dunedin
Stewart Island
(Aupourian)
(Cookian)
northern
elements
universal element ?
southern
elements
(Cookian)
(Forsterian)

geographic provinces has been strongly criticised by Dell (1962). His criticisms may be divided into two categories: criticisms of the entire concept of faunal provinces, and criticisms of the applications of the concept to New Zealand coasts.

It is Dell's contention that the data on distributions are not extensive enough to warrant the interpretations that have been made, particularly as applied to the area of overlapping distributions that is commonly labelled the Cookian province, that the criteria of endemism, centres of distribution, and limits of distribution, have not been applied in an uniform manner, that species from entirely different environments have been lumped together indiscriminately in compiling distributional lists, and that there is no correspondence between the provincial boundaries and any physical or historical boundaries. He supports these contentions with numerous examples and points out that not all of the criticisms apply to the same degree to all previous studies.

In criticising the entire concept of biogeographic provinces, Dell points out that there is no agreement between authors concerning the criteria for defining a province and that the provinces described by New Zealand authors would not satisfy any of the more common definitions.

The province concept, indeed any biogeographic concept, would seem to have two aims; descriptive and analytical. It is convenient, for several reasons, to be able to divide the world into areas that have similar characteristics. Geographically, this is done on the basis of physical and political boundaries. Biogeographically, it is done on the basis of similarities between animal and plant populations. Similarities in plant and animal distributions are usually associated with similarities in environment and consequently have boundaries coincident with physical features of that environment. To define areas of similar plant and animal distribution, Woodward (1866) defined a "province" as an area in which over 50% of the species are endemic. This criterion certainly ensures that the area is biologically distinct from any other area. Others have not insisted on such a high level of endemism. Dell (1962) has pointed out that the provinces defined by New Zealand authors do not reflect a high level of endemism and that no obvious physical foundaries coincide with the boundaries that they have defined. On the other hand, the province depicted by Hedgepeth satisfies the criteria of endemism and physical boundaries. The physical boundaries being associated with ocean currents of different temperatures and origins.

Similar criticisms of the province concept are implied in a more general treatment of marine biogeography by Hedgpeth (1957). Hedgpeth does not reject the province concept but points out the difficulties inherent in trying to assess the boundaries of a province. His concept of a province is obviously that of a larger geographic area than that used by New Zealand authors. Hedgpeth's map, Littoral Provinces of the World, places all of the South Island of New Zealand and the southern part of the North Island (corresponding to the Forsterian and Cookian provinces) in an Antiboreal province related to Tasmania and the southern tip of Australia. The northern half of the North Island (corresponding to the Aupourian province) is placed in a Warm Temperate province related to the southeastern and southern coasts of Australia. This would be in agreement with the interpretation of the relationships between New Zealand and Australian littoral flora and fauna given by Powell (1961a) and Knox (1963a).

Before attempting any further analysis of species distributions, in terms of provinces, it would be well to examine the concept of a province in the light of what we demand from this concept. After examining the usefulness of the concept, it should be easier to determine the criteria for defining a province.

Descriptively, is there any advantage in defining a set of smaller provinces within the limits of these provinces of Hedgpeth?

All of the New Zealand authors agree that there is a northern and a southern element in the distribution of New Zealand coastal species and that these elements overlap. A wide area of overlap would be expected if the northern and southern elements were considered as part of the two larger provinces. It would be as easy to label the northern and southern ends of New Zealand as parts of two larger provinces and to recognize the overlapping nature of the boundary area as to define three distinct provinces. Defining ever smaller provinces becomes cumbersome, as each province must be defined quite elaborately, whereas, it is easy to speak of a northern distribution, a southern distribution, and an area of overlap. Further, as the size of the provinces defined becomes smaller, a new problem arises. In order to maintain distinct areas with a high rate of endemism, it becomes necessary to take into account a larger number of physical boundaries. Archibenthal species have a wider and more uniform distribution than littoral species (Dell 1962). Consequently, it becomes necessary to have more littoral provinces than shelf provinces. Rocky shore organisms

have different distribution patterns than sandy beach organisms hence, the necessity for rocky-shore littoral provinces and sandy-beach littoral provinces. The different taxonomic groups have different dispersal abilities, and different ecological requirements so, it becomes necessary to have rocky-shore, littoral, molluscan provinces, rocky-shore, littoral, barnacle provinces, rocky-shore, littoral, rhodophyceaen provinces, etc., until, for lack of agreement of ranges of various genera and species, we are forced to discuss the distribution of each species separately. This reductio ad absurdum argument is a strong argument in favor of retaining criteria of high levels of endemism and distinct physical boundaries in the definition of provinces.

From the viewpoint of descriptive value, there seems to be no advantage in defining a large number of provinces within New Zealand.

As an analytical tool, the province concept is applied to the problem of species dispersal and speciation. It can be used to develop theories or to evaluate theories based upon paleontological evidence, genetic evidence, and geological evidence.

Finlay (1925), Powell (1961), Fleming (1962), and Knox (1963b) have discussed the distribution of New Zealand intertidal species in the light of the geological and paleontological evidence. It appears that the New Zealand land mass has been much altered during its geological history and that its present topography is very recent, dating only from the late Pleistocene. It also appears that much of the early flora and fauna was destroyed during Pleistocene glaciation. Thus, the current species have had to evolve from the survivors of the glaciation or from recently immigrated species.

Unfortunately, many of the shore species do not leave adequate fossil records. This is particularly true of the macroscopic algae, with the notable exception of the coralline species. Fleming has divided the current flora and fauna into elements according to their historical origins, three of which account for the majority of coastal species. The Malayo-Pacific element includes tropical and sub-tropical forms that appear to have immigrated to New Zealand from Pacific areas other than Australia. The Neoaustral element includes southern, cold-temperate, circumpolar species dispersed by the West Wind Drift. The Australian element includes such species that have arrived at New Zealand <u>via</u> Australia.

The Australian element is regarded as the most important element with regard to shore species and is apparently still operational.

As the Australian element in New Zealand shore species is so important, it would be well to consider what is known, or has been postulated, about littoral species distributions in Australia. A recent series of papers (Bennet and Pope 1953, 1960) (Womersley and Edmonds 1958) (Womersley 1960) have enlarged upon the distribution of littoral species from eastern and southern Australia and Tasmania, in terms of biogeographical provinces. The results of these discussions are summarized by Knox (1960, 1963a).

Three areas of the Australian coasts are of particular interest when considering the relationship with New Zealand coasts. These areas are defined by Womersley (1960) as: the Peronian province, an area of warm temperate waters including the coast of Queensland South of 25° S Latitude, the coast of New South Wales, and the coast of eastern Victoria; the Flindersian province which includes the southern coast of Australia from southwestern Western Australia to Victoria and the entire coast of Tasmania; the Maugean sub-province of the Flindersian province which

is that part of the southern Australian coast from just East of Robe, South Australia, the Victoria coast and the Tasmanian coast. Bennet and Pope (1960) consider these three areas to be separate provinces and would raise the Maugean sub-province of Womersley to full provincial status.

Dellow (1955) has compared the algal population of the New Zealand Aupourian province with that of the Peronian of Australia. Powell (1961) also comments on the number of Peronian molluscs found in the New Zealand Aupourian province. Womersley however states that the New Zealand Aupourian province is related to the Australian Flindersian province and that the differences between the Cookian province and the Aupourian province are similar to those between the Flindersian sub-provinces. It is apparent that the New Zealand Forsterian province has no analog in Australia. Bennet and Pope point out that the Maugean province, or sub-province, is an area of cool temperate water and that no part of the Australian coast extends into the cold-temperate waters as does southern New Zealand. However, some of the elements that are shared by the Forsterian and Cookian provinces are the same elements that can be related to the Maugean province of Australia.

It is of interest to note that the Kaikoura Peninsula

resembles the Australian coasts described by Womersley (1960) in more ways than some of the other coasts of central New Zealand. There is a lessened prominence of the mussel species, the absence of a Bostrychia band, and a reduction in the barnacle population similar to that of the Victorian and Tasmanian coasts.

From the biogeographical treatises cited, we can extract certain general trends upon which the authors are in agreement. The northern New Zealand coastal flora and fauna have received contributions from the Australian Peronian and Flindersian provinces. The southern coasts have received contributions from the Flindersian and Maugean provinces (or sub-provinces), as well as having cold-temperate elements not related to the Australian coasts.

Bennet and Pope (1953) point out a wide area of overlap of species between the Flindersian province and the Maugean province and Womersley has compared this region of overlap to the central New Zealand coast. Further, while both of the distribution centres of New Zealand are related to the Australian Flindersian Maugean overlap, they themselves overlap. It is no wonder then that there have been difficulties in determining biogeographical boundaries for New Zealand coastal provinces.

Caughley (1964), in an amusing and rather penetrating commentary on New Zealand zoogeography, has pointed out that the New Zealand vertebrate species are mainly ones that could have been predicted to be here, on the basis of principles of dispersal, before they had been catalogued. Applying his method of reasoning to shore species, we would expect to find certain features. With a geological history of climatic shifts from sub-tropic to sub-antarctic we would expect to find species of considerable antiquity from both sub-tropical and sub-antarctic assemblages. The numbers of such species would not be expected to be high because of the fairly recent glacial period. Because of the glacial action, we would expect to find a strong influx of post-glacial species from areas upstream in the neighbouring oceanic currents. Major currents approaching the New Zealand shores are: the East Auckland Current and the East Cape Current, derived from the Trade Wind Drift, following the east coast of the North Island from Cape Reinga to the vicinity of Cape Mahia; the West Auckland Current, also derived from the Trade Wind Drift, which comes a short distance down the west coast of the North Island; the Westland Current, derived from the East Australian Current, flowing northward along the west coast of the South Island and branching at

Cook Strait to form the D'Urville Current eastward through Cook Strait and the northern branch which meets the West Auckland Current in a convergence area of varying position; the Southland Current of mixed sub-tropical water from the East Australian Current and sub-antarctic water from the West Wind Drift, which flows through the Fouveaux Strait and up the east coast of the South Island; the Canterbury Current, largely sub-antarctic water originating from the West Wind Drift, flowing from Banks Peninsula, past Kaikoura, and up the east coast of the North Island to meet the warm East Cape Current in a large area of convergence of varying position (Knox 1960).

From these current patterns, we would expect to find a concentration of recently immigrated sub-tropical forms on the North Island north of the most northern positions of the convergences. We would also expect to find a concentration of cold water forms at the southern end of the South Island and along the east coast to the southern limit of the convergences. Finally, we would expect that species with the widest temperature tolerance from both concentrations would have spread throughout the range of position of the convergences. It might be further expected that the southern area would have a greater mix-

ture of forms than the northern because both sub-tropical and sub-antarctic waters are involved in the Southland Current but only sub-tropical waters are involved in the East Cape and East Auckland Currents. This, it would appear, is largely what we do find.

In such an analysis, there is no need to, nor convenience in, referring to the province concepts that have been applied to the New Zealand coasts. However, we do find an explanation of the difficulties that have been encountered in defining such provinces. It appears that the usefulness of the province concept in New Zealand is limited to tenuous descriptive functions. It is explicitly stated, or implied, in all of the cited works that the concept of New Zealand shore provinces has extended to, or somewhat beyond, the point of usefulness and that what is currently of concern is the need for more work on distributional data, taxonomic clarification, and autecological analysis.

Analysis of Field and Experimental Observations Related to Distribution Patterns

Introduction

It has been pointed out by V.J. Chapman (1946, 1957) that there are in existence enough descriptive papers to convince us of the universal nature of shore zonation and that now we need more autecological studies to help shed some light on the mechanisms responsible for this zonation. There remains, however, a need for the general descriptive paper. It serves the recent arrival as an introduction to the area, it provides a base from which further studies can be made and changes observed, and serves as an item of data for the biogeographer and the reviewer. It is hoped that this paper will serve these purposes and, by contributing original research of an ecological nature, serve them well.

The previous sections contain a description of the general physical features of the Kaikoura Peninsula and of the adjoining waters. A more specific description of the flora and fauna of the intertidal region followed. In this section, an attempt will be made to correlate that information with studies of other shores, by other investigators, and with local experimental results in order to present an orderly and unified account of the major environmental factors and their effects on the dominant organisms.

Certain species, or groups of species, are more obvious on the shores because of their size or numbers. These species are generally referred to as "dominants". They have been labelled as "topographical dominants" in this paper to keep the writer, and perhaps the reader, mindful that this

dominance is only apparent, is only the result of visual impact and not necessarily indicative of any superiority or importance relative to less conspicuous species. At Kaikoura, these topographical dominants are: the littorinids Melaraphe cincta and M. oliveri, limpets mainly of Cellana spp., the barnacles Chamaesipho brunnea, C. columna, and Elminium plicatus, a trochid Melagraphia aethiops, a turbonid Lunella smaragda, the rhodophyte Porphyra columbina, the fucoids Cystophora torulosa, Durvillea antarctica, and Horosira banksii. Of this list, only E. plicatus and D. antarctica have been ignored. The loss is not as great as it may seem as these two species are only dominant in the most surf-beaten areas. It may also be partly excused by the attendant difficulties of establishing and maintaining experiments in these precarious locations. As there are extensive studies currently being made of Cellana spp. and of the barnacle species less emphasis was placed upon them for this paper.

Other organisms are considered as they occur in the routine of the field experiments.

It has been generally accepted that the regular vertical movement of the water-line caused by tidal action and wave action has been the primary, indeed the essential, cause of vertical zonation of organisms on the sea shore. Stephenson advanced the argument that a zonation would occur, and indeed does occur, where tidal action did not exist. The existence of a zonation pattern at the edge of fresh-water lakes and in marine situations with little or no tide action was attributed to the interface between the air and the water where gradations of humidity and light occur.

Many authors have taken exception to this and have pointed out that the zonation of most marine shores can be correlated to the vertical rise and fall of the water level caused by the tide and modified by wave action.

Southward (1958) points out that this problem is largely semantic and that both parties are correct. He makes the distinction between the absolute existence of zonation and the "observed patterns of zonation" and advanced the opinion that tidal action is the main cause of the observed patterns of zonation.

The mechanisms by which tidal rise and fall effect the distribution of organisms are far from well known. Investigations of this problem have generally fallen into two categories: descriptive accounts of the zonation of localities which are related to descriptive accounts of the tides and other environmental factors of that locality, and experimental studies of specific organisms and their reactions to certain environmental stresses that are supposed to be related to the tidal action. Coupled with these studies have been several general reviews and papers of biogeographical nature which have performed a great service in correlating facts and ideas.

Having accepted the proposition that the observed pattern of zonation is related to the tide, we must examine the reactions of individuals of various species to the stresses caused by the tides. Then we must study the distributions of the species on the shore in relation to these stresses and in relation to other external factors affecting either the organism or the tide levels.

Such factors would include wave action which has an effect upon the level of the tide and interspecific reactions which might limit, or extend, the tolerance of the organism to tidal factors.

In this way we can hope to arrive at a better understanding of the mechanisms that cause the distribution of organisms in particular patterns on the shores.

Tides

Here, it is proposed that the effect of tidal action be dealt with under two headings: submergence and emergence.

Submergence

Many authors have made the point that there is a relationship between the degree of exposure to air and the level of organisms on the shore. Very few however have bothered to point out that there is an equally strong relationship to the degree of submergence, nor have they pointed out that while the degree of exposure to air may account for the upper limits of species on the shore it does not account for the lower limits. And yet, each distribution must have both limits.

It was felt necessary to test the hypothesis that submergence imposes a lower limit on the distribution of adult intertidal organisms (Appendix 2).

i. Porphyra columbina was out of season at the time of the testing. Barnacles were not tested because their sessile nature indicates that the problem of their existence sublittorally would involve juvenile forms rather than adult forms.

Field observations showed that it was not necessary to test Lunella smaragda, Cystophora torulosa and Hormosira banksii. L. smaragda and C. torulosa have naturally sublittoral distributions and can obviously withstand total submergence. H. banksii is found down to ELWS in sheltered spots and in totally submerged conditions in many tidal pools. Therefore, it would seem that H. banksii can withstand total submergence and that some other factor is responsible for its lower limit.

ii. As a consequence of the experiments performed on M. aethiops, M. cincta, M. oliveri, C. denticulata, C. flava, and C. radians, it was concluded that only the Cellana spp. were unable to survive total submergence (Table 5).
iii. Studies on H. banksii (Trevarthen 1954) and on other algae (Baker 1909) (Shelford and Gail 1922) indicate that many algae have a decreasing efficiency of photosynthesis with increased depth and that others have optimal conditions in shallow water. Trevarthen postulates that this decreased efficiency is the cause of the lower limit of H. banksii. However, this does not explain why the same sequence of plants is found in neighboring areas even when there is a difference in the tidal range and therefore a difference in the absolute depth of water with which the plants are covered at similar tide levels, e.g. EHWS ELWS.

So, the hypothesis that submergence is directly responsible for the lower limits of distribution is not proved for any species and is, in fact, disproved for all species tested except the Cellana spp.

Table 5

Relative survival of total submergence

Field observations

(a) Lunella smaragda .....infra-littoral distribution

(b) Hormosira banksii .....pool bottom distribution

(c) Cystophora torulosa .....infra-littoral distribution

Aquarium experiments

(d) Melaraphe cincta .....30 day survival

(e) Melaraphe oliveri .....30 day survival

(f) Melagraphia aethiops.....45 day survival

(g) Cellana spp. .....2-10 hour survival

Not tested

(h) Chamaesipho columna

(i) Elminius plicatus

(j) Porphyra columbina

Emergence

The primary event of tidal recession is to cause the sea to retreat from over part of its bottom, exposing a scene every bit as spectacular as that which greeted the ancient Jews when, at Moses command, the Red Sea rolled back (Exodus 14: 21,22). Here are exposed thin-skinned animals and odd appearing thallophytes, clearly related to, often nearly identical with, species that never leave their marine environment alive. Yet, every receding tide leaves them bathed in air, rather than water, at atmospheric pressure rather than supported by submerged pressures, and on alternate tides (if semi-diurnal, as at Kaikoura) exposed to bright light and sharply raised temperatures. It appears no less a miracle that these myriad forms should survive and thrive where the sea is not, than that the ancient Jews should have passed once where the sea was not.

i. One of the prime concerns of most of the early students of zonation was with the effect of desiccation and increased temperatures on the shore organisms. Doty (1940) and Doty and Archer (1950) demonstrated a marked correlation between the distribution of certain shore algae, the sharp changes in exposure time, and the ability to withstand desiccation.

i. Montford (1937) and Biebl (1952) have shown that the degree of tolerance to desiccation is greater among certain high level species of algae than among other low level species. Zaneveld (1937) demonstrated a progressive thickening of the cell walls of fucoids that corresponded to the position of the plants on the shore.

Investigators of shore fauna have often found similar relationships. Broekhuysen (1941) found a graded resistance to drying and to high temperatures in some South African molluscs. Clark (1957) found similar relationships between Melagraphia aethiops, Zediloma atrovirens, and Z. digna. However, other investigators have found that this graded response is not always the rule. Evans (1948) found no such relationships among the British molluscans.

What then is the relationship between desiccation factors and the species being considered at Kaikoura? Do their resistances to desiccation have the same order as their positions on the shore?

ii. Experiments carried out on Melaraphe spp., M. aethiops, and Lunella smaragda (Appendix 2) indicate not (Table 6). The resistance to desiccation of Melaraphe spp. and other related littorinids is well-known.

Incidents of prolonged storage of littorinids with subsequent recovery are not uncommon in the literature. It proved to be impractical to carry on with the desiccation experiments until a 50% lethal point had been reached for Melaraphe spp. The other animals had died days before the first signs of distress were noted in Melaraphe spp. It seemed safe to conclude that the presence of Melaraphe spp. in

large numbers in the littoral fringe well above the other macroscopic forms was due to a superior ability to withstand desiccation.

M. aethiops, which occurs higher, and drier, on the beach than L. smaragda, proved to be considerably more susceptible to heat and drying (Table 6). The times and temperatures involved in the experiment would indicate that there may be a modifying factor influencing the upper limit of M. aethiops, that desiccation alone was not responsible.

iii. That L. smaragda had not reached the limits allowed by its resistance to heat and drying was evident. In the field its upper limit is always below that of M. aethiops. Further, on the shore it is generally found in hidden places, pools, crevices, or under sea-weeds. Night observations have shown that it is a very mobile animal, as is M. aethiops, but that it has little tendency to extend its range upwards during nocturnal grazing.

Table 6

Relative Survival of Desiccation in Air at 35°C.

50% mortality point as determined by recoveries

(a) Melaraphe cincta .....over 120 hrs.

(b) M. oliveri .....over 120 hrs.

(c) Lunella smaragda .....60-65 hrs.

(d) Melagraphia aethiops.....40-60 hrs.

Total mortality of plant tissue

(e) Hormosira banksii .....6-8 hrs.

(f) Cystophora torulosa .....6-8 hrs.

Inferred by comparison with another species

(g) Porphyra columbina .....12-14 hrs.

Not tested

(h) Chamaesipho columna

(i) Elminius plicatus

(j) Cellana spp.

In dealing with the effects of emergence on the distribution of mature organisms we immediately run into the problem: what is maturity? We have also made a necessarily arbitrary decision to sidestep the problems of settlement, which in nature can not be separated from the adult life of the organism. To avoid some of the errors inherent in ignoring juvenile stages, it was decided to apply some of the experimental techniques to various size classes of animals.

Attempts to class Melaraphe cincta and M. oliveri by size groups proved futile and frustrating. However, certain interesting observations were made about distribution of Melaraphe spp. There seemed to be no grading of organisms by size in relation to level, or degree of emergence, on the shore. However, there is a size grading with regard to degree of exposure to wave action (Fig. 20).

It appears that Melaraphe spp. may under favourable conditions be capable of more growth in one season than is common in several seasons in more severe locations. There appears to be a limit on size imposed by the conditions. As a consequence, no size groups that might indicate age classes were evident.

Volume measurements of M. aethiops collected along shore transects at Wairepo Flats were made. The total curve of all collections (Fig.21) indicates four definite size classes and a probable fifth. This date corresponds with the results of similar studies by Clark (1957). On boulder beaches Clark found five size classes which he demonstrated to be year classes. Analysis of the size classes at individual stations along the transects (Fig. 22) gave size distribution date that also correspond to that found by Clark.

Melagraphia sprat settle along the entire intertidal range then migrate towards a central range. Those that do not reach this central range perish. The first year class stay well sheltered in runnels, pools, and under rocks. Older groups come out in the open and extend their range vertically, both upwards and downwards.

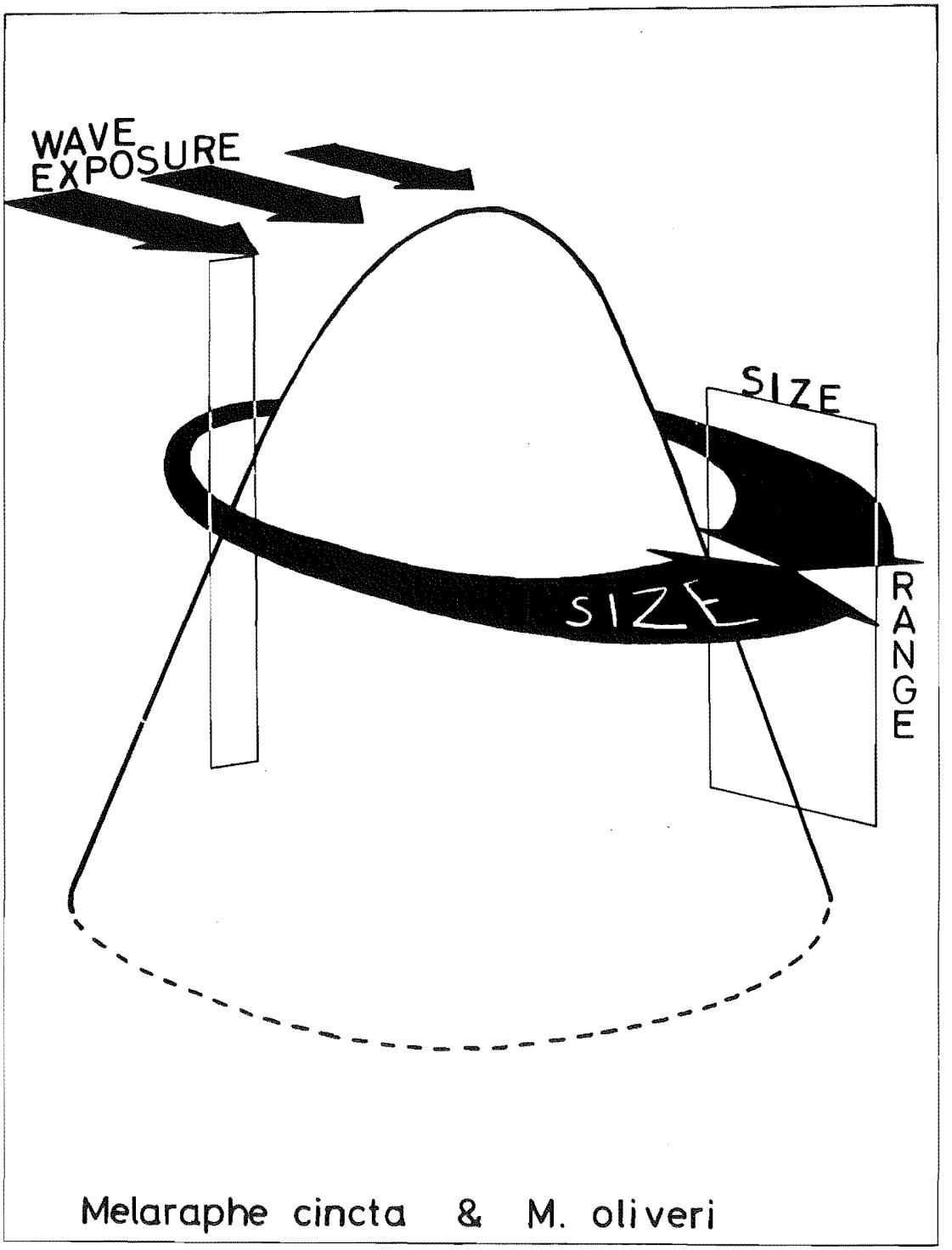
Desiccation experiments were performed upon M. aethiops to determine the relative susceptibility of various size classes. The results, as shown on Table 7, indicate that there is a definite increase in desiccation tolerance with size and age as would be expected from the field observations.

Similar collections were made of L. smaragda. Volume measurements swparated two distinct size classes within the littoral zone (Fig. 23). It was felt that a third size class was present in the few specimens above 70 ml. These individuals are twice as big as those represented in the second spike of the graph and are, at least, as much bigger than the individuals of the second group, as the second group individuals are bigger than those of the first group. The numbers of large individuals collected was not great enough to support this hypothesis, or to disprove it. However, collections made at other points, notably at the Oaro sublittoral platforms south of the Kaikoura Peninsula, and observations made while skin-diving show that large numbers of these and even larger individuals are present in the sublittoral zone. The distribution on the shore of the size classes postulated was plotted (Fig. 24). This distribution indicates that the smallest L. smaragda are limited to the littoral zone and that the larger individuals are found lower on the shore.

Table 7

Melagraphia aethiops desiccation tolerance at 35°C.

	Survival %	
1st year class	2d & 3d year class	4th year class
22 hrs 50%	100%	100%
36 hrs 0%	90%	80%
40 hrs 0%	70%	40%
49 hrs 0%	20%	20%
59 hrs 0%	20%	40%
66 hrs 0%	0%	0%



Melaraphe cincta & M. oliveri

Figure 20.

A diagrammatic representation of the decrease in size and increase in vertical range of Melaraphe spp. corresponding to an increase in wave exposure, as observed on isolated rock masses.

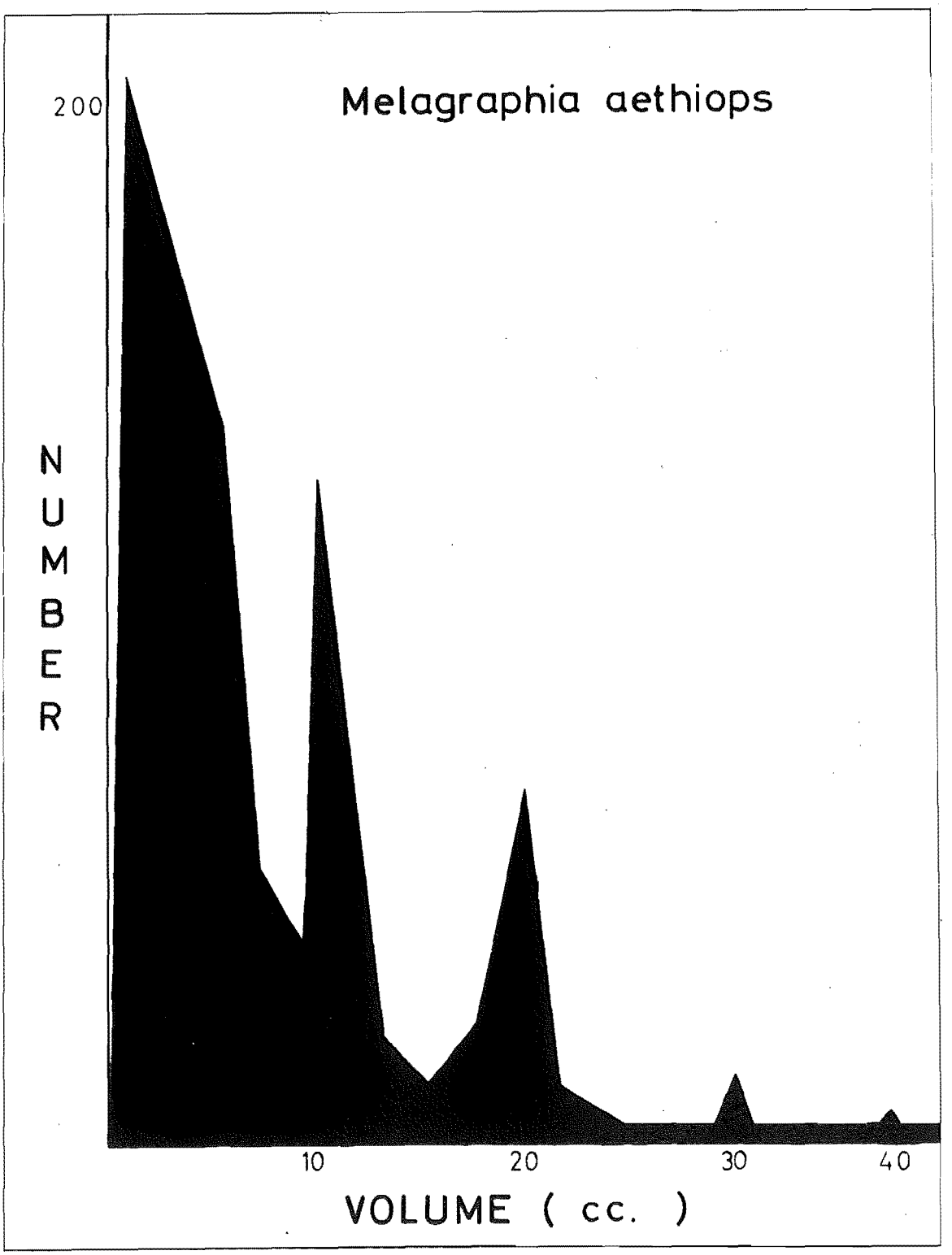

Melagraphia aethiops
200
NUMBER
10
20
30
40
VOLUME (cc.)

Figure 21.

A graph representing size classes of Melagraphia aethiops collected at Wairepo Flats during the month of October, 1964.

Melagraphia aethiops

Figure 22.

A graphic representation of the distribution of size classes of Melagraphia aethiops on the shore. Data collected at Kaikoura in 1964 and supplemented by information in Clark (1957).

The particularly restricted range of the survivors of the first year and the consequent spread in range of the larger individuals is shown.

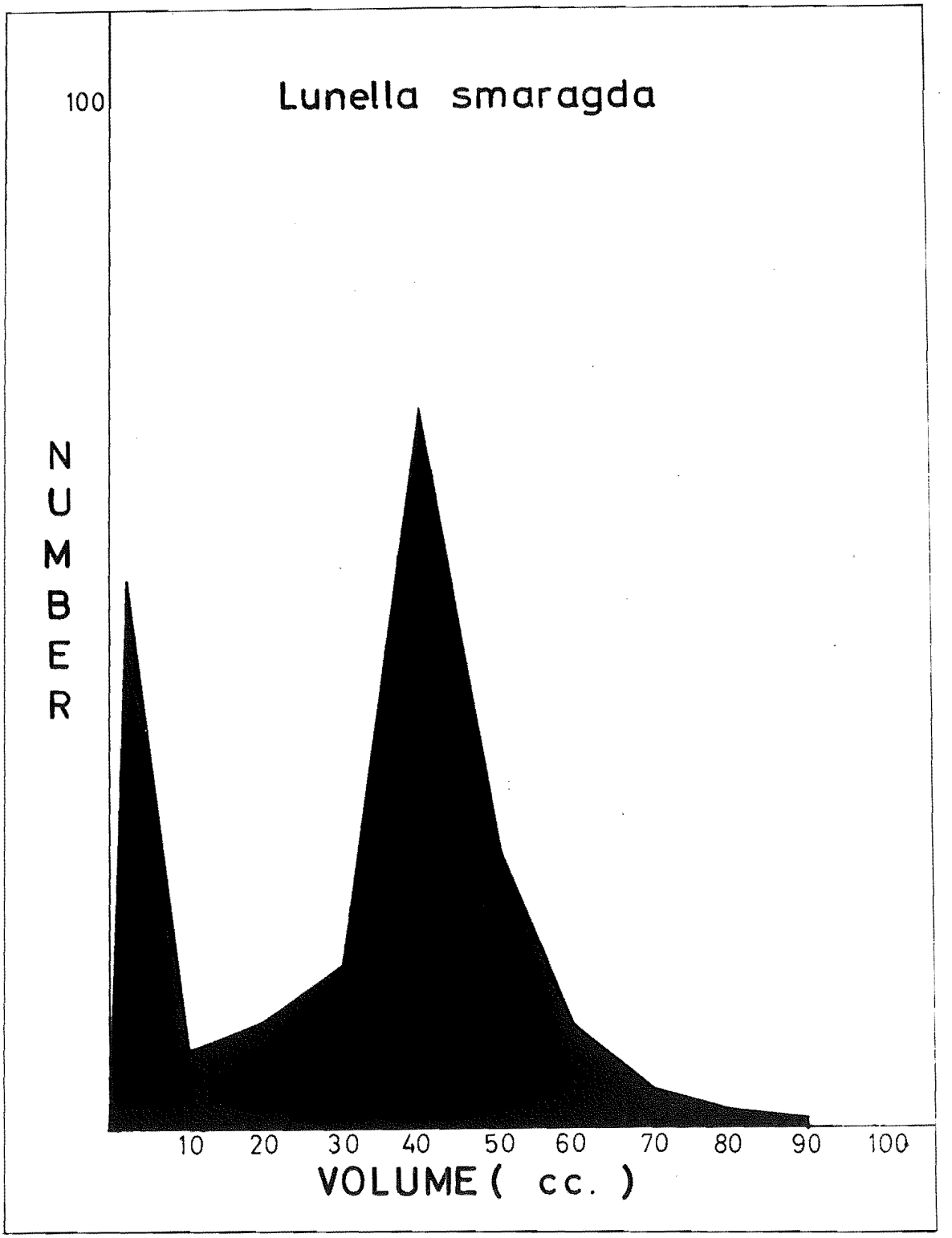

Lunella smaragda
100
NUMBER
10
20
30
40
50
60
70
80
90
100
VOLUME (cc.)

Figure 23.

A graph representing the size range of Lunella smaragda collected on Wairepo Flats during the month of October, 1964.

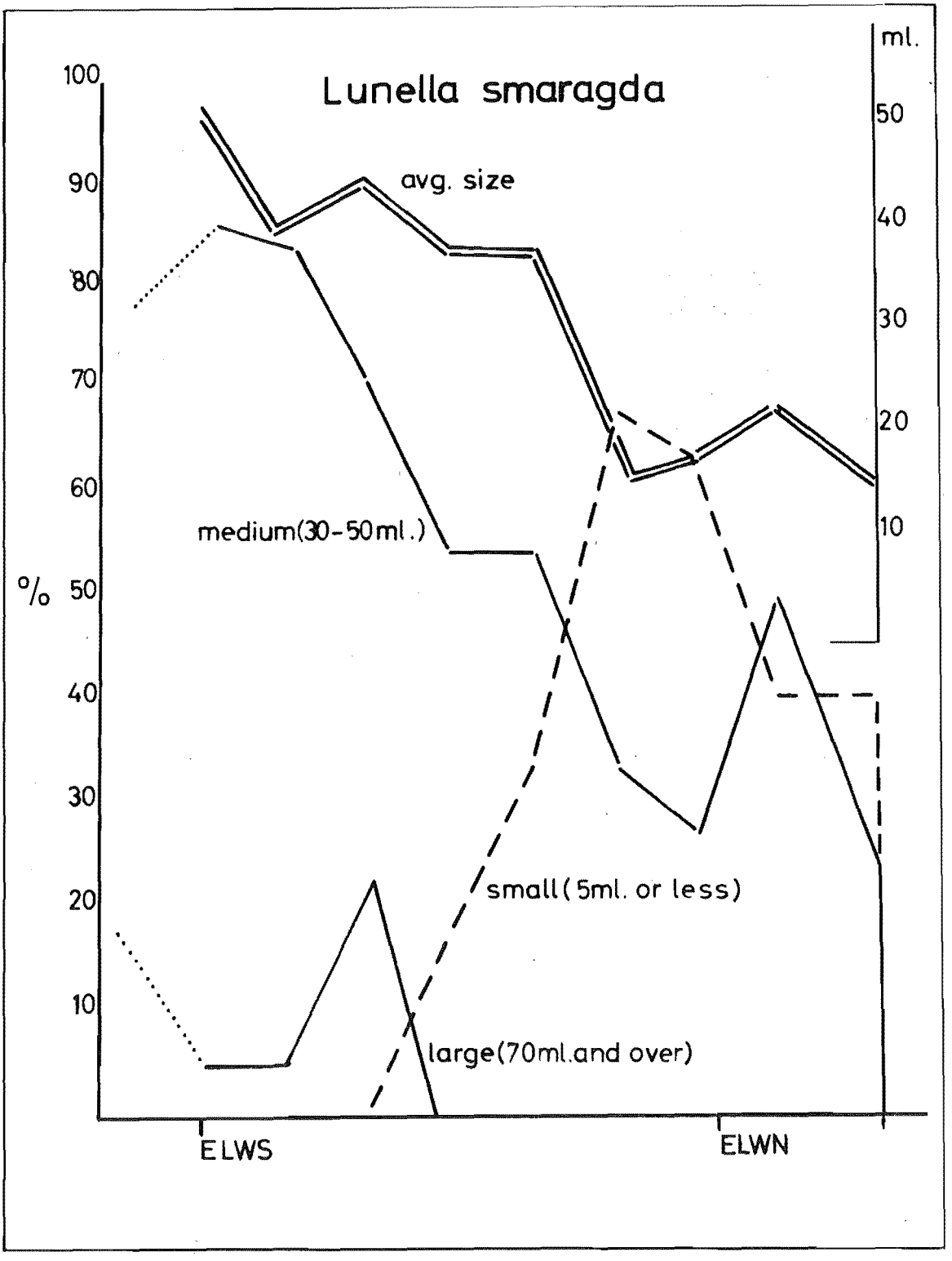

Lunella smaragda
avg. size
medium(30-50ml.)
small(5ml. or less)
large(70ml.and over)
%
ml.
100
90
80
70
60
50
40
30
20
10
50
40
30
20
10
ELWS
ELWN

Figure 24.

The distribution of three size classes of Lunella smaragda on Wairepo Flats in October, 1964. The limitation of the smallest class to the littoral zone and the tendency of the larger individuals to occur near the sublittoral is clearly shown.

Not shown are the even larger size classes that have been observed sublittorally and are not found in the littoral zone at Kaikoura.

It further indicates that the largest individuals are lowest on the shore and are only the upper edge of a sublittoral population of the very largest specimens of L. smaragda. That the largest individuals are the most resistant to desiccation and salinity dilution was evident from the laboratory experiments and was not further tested. So the most tolerant individuals of the most tolerant species (of those tested) appear to migrate away from the area where this tolerance might be useful.

The algal series chosen, Porphyra columbina, Hormosira banksii, and Cystophora torulosa, showed a more definite relationship between their upper limits and their ability to withstand drying.

Though Porphyra fronds are very thin (two cell layers), its habit of convoluting and overlapping in many layers enables it to hold large quantities of water which prevent its desiccation.

Experiments performed in California (Rasmussen, unpublished data) on P. lanceolata, (Setch & Hus) G. Smith which has a similar form and habitat showed that single fronds are very susceptible to desiccation but that two or more layers will hold enough water to resist damage up to forty-eight hours. Single layers closely adpressed to the rock will similarly hold enough water to survive well beyond the exposure afforded by normal tidal conditions.

The results of the experiments on H. banksii and C. torulosa were not conclusive. Tests to determine the viability of the experimental plants failed in every case. Revival methods indicated a similar death point for each alga (Table 6).

An indication of relative damage may have been indicated by the degree of discoloration in the experimental plants. Discoloration occurred in both species and the amount of discoloration was proportional to the amount of desiccation. The discoloration first appeared in C. torulosa. Total discoloration occurred at some unknown time, between observations, for both species. It appeared that the discoloration proceeded at a geometric rate, possibly logarithmic. Field observations show this discoloration occurs commonly in the upper range of distribution of each species.

Field observations of H. banksii showed a progressively stunted growth towards the top of the range and an extension of range in such places that collect moisture. This range also corresponded exactly with the limits of Corallina officinalis. Wherever there was H.banksii, there was an undergrowth of C. officinalis. H. banksii, however, did not appear on every bit of C. officinalis.

Trevarthen (1954) concluded that the upper limit of H. Banksii was due to desiccation and, with a minor exception that will be discussed later, I see no reason to disagree.

Field observations of C. torulosa also show a progressive stunting of growth in the upper reaches of its range. Further, growth rate experiments (Appendix 2) indicate a very slow growth at the upper edge of the range.

It may also be noted that there is an extension of the range of C. torulosa in those shore areas where H. banksii is found in heavy concentration (Fig. 41). This has the appearance of a nursery effect.

The small C. torulosa lie under the Hormosira banksii when the tide is out and are protected from drying out. When they are big enough to protrude from this nursery bed the growth drops off, or stops, and evidence of discoloration is found on such projecting plants.

Removal of the H. Banksii from areas where the two species overlap brought a quick demise of the C. torulosa and no further establishment of young plants (Appendix 2).

Therefore, it was concluded that desiccation was the major, if not the only, limiting factor preventing C. torulosa from extending its range up the shore.

Component factors of emergence, particularly desiccation appear to account for the upper limit of distribution of several species. In the plant series, P. columbina is the most resistant to desiccation and has the highest vertical range. H. banksii appears to be more resistant than C. torulosa judged by field observations. This is only slightly indicated by laboratory experiments but is in accord with what might be expected from the structure of the plants. H. banksii is a hollow structure filled with a mucilaginous fluid (Osborn 1948) (Trevarthen 1954). C. torulosa has solid tissues (Nizzamuddin 1964).

Comparison of weight losses during desiccation experiments (Appendix 2) indicate that H. banksii has a more rapid initial loss of weight, as might be expected. The dimpling of the vesicle observed during the desiccation indicated that this loss was from the vesicle fluid. The slightly slower and more even rate of loss from C. torulosa coupled with the observation of earlier discoloration of the tissues would seem to indicate that the fluid loss was directly from the tissues.

and that cell damage was occuring.

In the animal series, Melaraphe spp. were obviously the most resistant to desiccation, which is in keeping with their position on the shore. M. aethiops also occupies a range that seems compatible with its desiccation tolerance. However, L. smaragda apparently is very tolerant of desiccation, more than its range would indicate. Some other factor should be sought to explain its upper limit.

Finally, another component factor of emergence was tested. The animal series was subjected to a series of freshwater dilutions of sea water. The results (Appendix 2) indicate that Melaraphe spp. are very tolerant of dilution. This is confirmed by field evidence. Melaraphe spp. are found in large numbers near fresh water seepages and drains. The presence of such seepages extends their upward range. Thus the dilution caused by seepage or rainfall on the upper shores would in no way inhibit the upper extension of Melaraphe spp.

M. aethiops and L. smaragda both withstood more dilution, for a longer period, than they are likely to receive on the Kaikoura shores. Again, L. smaragda proved to be considerably the more tolerant organism which is inconsistent with its position on the shore.

No gain could be seen in testing the plant series against this factor.

Wave

i. Studies in all parts of the world have shown that certain changes in the pattern of species banding and, ultimately, in zonation are related to the degree of wave action acting upon the shore and the organisms. The relative time of submergence and emergence of the organisms is altered by wave action to form what have been called "effective tide levels" which may be substantially different from theoretical tide levels.

Various attempts have been made to measure the physical effect of wave action in terms of the wetting and exposing of levels of the shore and correlating these measurements to the observed changes in the vertical distributions of the organisms. A notable example of this approach is Morgans' (1957) analysis of four transects at False Bay, South Africa. Measurements of "upwash" and "suck back" were made at sites of varying exposure to wave action and related to the upper and lower limits of prominent organisms and to their centers of distribution. Morgans found that the effect of upwash was to raise the concentration of the organisms by nearly the actual distance of the upwash and that this positive raising of the level on the shore was a relative lowering in relation to the effective tide level formed by the upwash.

Other workers have attempted to measure the effect of wave action in other ways. The main problem in this approach has been to find an accurate measure of the upwash, or "swash" (Southward 1953). Frequently cited measurements of wave action are those of Moore (1935) Colman (1933), and Southward (1953). A review of the problem of the mechanical measurement of waves has been written by King (1959).

A different approach to the problem was made by Ballantine (1961) in which he accepted that the exposure to wave action affects the vertical distribution of the organisms and asserts that the delicate measurements required to determine the degree of exposure on a physical basis, are currently beyond our reach. He proposes that the most delicate assay of the wave factor is the one made by the organisms themselves and proposes an exposure scale based upon the distribution of the organisms.

All the previous studies indicate that the effects of increased wave action may be summarized as follows:

(1) A general upward shift of the concentration center of most species in the eulittoral and littoral fringe.

(2) A vertical extension of the range of each species.

(3) A relative lowering of the concentration centers of species in the upper sublittoral and of some species in the lower eulittoral.

(4) The disappearance of many species that appear to be intolerant of wave action.

(5) The appearance of a few species that appear to require or tolerate wave action.

The information acquired from the survey transects and from the analysis of wave action in the earlier sections of this paper have been co-ordinated to determine how the distribution of species on the peninsula fits the above summary and the Ballantine scheme.

ii. The physical and the more general biological characters of Ballantines (1961) scheme were combined with abundance scales being developed for New Zealand shores (Ballantine,

pers. comm.) and applied to the data previously collected from the Kaikoura transects. Based upon his survey of European coasts, Ballantine proposed an eight point scale ranging from (1), Extremely exposed, to (8), Extremely sheltered. This method has many advantages. It is based upon the concentration of a series of indicator organisms which can be determined for each region under investigation. It provides a scale that is biologically defined and suitable for comparing widely separated shores. On the basis of these scales, the Kaikoura shores range from (2) Very exposed, at very limited area of the tips of Seal Reef and Sharkstooth Point, to (7) Very sheltered, deep in the Mudstone Bay near the base of Sharkstooth Point. The largest part of the peninsula fell between (3) Exposed and (6) Sheltered.

The surf belt, labelled A on Fig. 6, of the wave analysis in this paper, contained shores rated as (3) Exposed, and the very limited areas that were rated (2) Very exposed. The belt labelled B represented shores rated (4) Semi-exposed on the Ballantine scale. Belt C included all the (5) Fairly sheltered shores and belt D represented the (6) Sheltered and the limited stretch of (7) Very sheltered. There appeared to be a nearly perfect 1:1 relationship between the results of the wind and wave analysis and the biologically defined scale of Ballantine.

The information gathered from the transects has been summarized on Figures 25-31 to show the effect of wave action on each species. In general the effects follow the expected pattern quite well. Close examination of the figures show several anomalies.

These are more apparent than real as will be shown by taking each species in relation to its total environment.

Figure 25 demonstrates three low level algae, Cystophora spp. (representing mainly C. torulosa), Carpophyllum maschalocarpum, and Durvillea spp. (D. antarctica at Lighthouse Point and Sharkstooth Point, D. willana at Seal Reef). The variations in level of Cystophora spp. are mainly due to lack of adequate substrate throughout the species range. Cystophora spp. all have a sublittoral distribution that is apparent only at the Wairepo Flats transect. At Waeroa Point and Laboratory Rocks a shelving of the rocks prevents the species from going higher than shown on the diagram. The extension at Mudstone Bay Flats is due to the nursery effect mentioned earlier, only the particular placement of the transect prevents this effect from showing for this position at Wairepo Flats.

The truncation of the distribution of D. antarctica at Sharkstooth Point is coincidental with the change in aspect at this level on the transect. At this level there are large broken rock masses at the base of the solid platform edge. The high distribution shown at Seal Reef- East represents D. willana which has a lower center of distribution wherever the two species are found in a mixed condition. This population is higher than expected. The end of transect is at one edge of a wide channel between rock masses. After each wave or swell enters the channel, it drains back at a furious rate and the water level is considerably higher than that outside the channel. Therefore the effective water level during the lower part of the tidal cycle is higher than the level in neighboring areas.

Figure 26 depicts the distribution of Corallina officinalis. The rise of the upper limit of C. officinalis is quite pronounced. The high levels reached upon the sheltered platforms are explained by the poor drainage of these very level platforms and by the heavy cover of Cystophora spp. and Hormosira banksii which form a moisture trap so that the rocks are not dry even when the tide is out. The correlation of H. banksii with C. officinalis has been mentioned in an earlier section.

The channel effect mentioned in connection with D. willana on Seal Reef-East is also evident here. The reason for the drop in level at Seal Reef - Northeast and at Sharkstooth Point is open to conjecture. These slopes are well-drained and directly exposed to sunlight from sunrise until past midday.

The distributions of M. aethiops and Lunella smaragda (Fig. 28) have been discussed, in part, in an earlier section. The distribution of M. aethiops appears much as expected. A rise in concentration and upper limit with a horizontal limit when the wave action becomes too heavy. The appearance of M. aethiops at Lighthouse Point is from a section of the transect that is sheltered by the parapet effect mentioned in the description of this location. The rating for wave action given to this transect reflects only the condition at the seaward face. Areas of the platform would rate much lower.

The L. smaragda distribution follows the heavy plant cover and favorable terrain. This is typical of a sublittoral organism that invades the eulittoral.

The distribution of Porphyra columbina (Fig. 27) follows the scheme outlined, in a classical manner. Some of the distributions are evidently truncated. This is because the rocks went no higher. H. banksii (Fig. 27) shows a strong favoritism for the sheltered platforms. Increased wave action and unsuitable substrate account for the scant distribution at Waeroa Point. Heavy concentrations at Avoca Point and Laboratory Rocks are due to stretches of platform that are more sheltered than the exposed faces of the platform.

There is little that can be said about wave action from Figure 29. The distribution represents the combined range and concentration of four species, Cellana denticulata, C. flava, C. ornata, and C. radians. These species represent a large proportion of the grazing molluscs of the eulittoral and as such will be of great interest in a later section.

Figure 30, showing the barncle distributions and Figure 31, showing the littorinid distribution represent the effect of increased wave action very well. The rising centers of concentration are particularly obvious in Chamaesipho columna and the Melaraphe spp. Truncation of the substrate can be traced through the truncated distributions diagrammed. The low distribution of C. columna at Sharkstooth Point-West reflects the aspect of the substrate (Fig. 7) where the surface is a slight overhang and thus drains instantly. The transects at Lighthouse Point and Sharkstooth Point-East show the spearation of barnacle species where they occur together.

It is evident, at this point, that the factors related

to the alternate emergence and submergence of the shore by the tides and modified by wave action have a distinct causual relationship with the distribution of organisms on the shore. The upper limits of several organisms have been shown to be related to their ability to withstand desiccation. The horizontal limits of several species have been related to the mechanical effect of wave action. However, there has been little indication that these factors affect the lower limits of vertical distribution, with the possible exception of Cellana spp. Also there are discontinuities and anomalies to account for in the upper limits that indicate the presence of other modifying factors.

The largest group of modifying factors probably are those grouped as interspecific relations. These include limitations on food supply, space and light competition, symbiotic effects, and predation. Interspecific relations will be considered in the following section.

Coralina officinalis
Pier 0
EHWS
MinHWS
EHWN
ELWN
MinLWS
ELWS
WAVE CLASS
D
C
B
A
10. Mudstone Bay Flats
3. Wairepo Flats
6. Seal Reef - West
12. Waeroa Point - Northwest
11. Waeroa Point - Southeast
2. Avoca Point
1. Laboratory Rocks
9. Sharkstooth Point - West
7. Lighthouse Point
4. Seal Reef - Northeast
5. Seal Reef - East
8. Sharkstooth Point - East

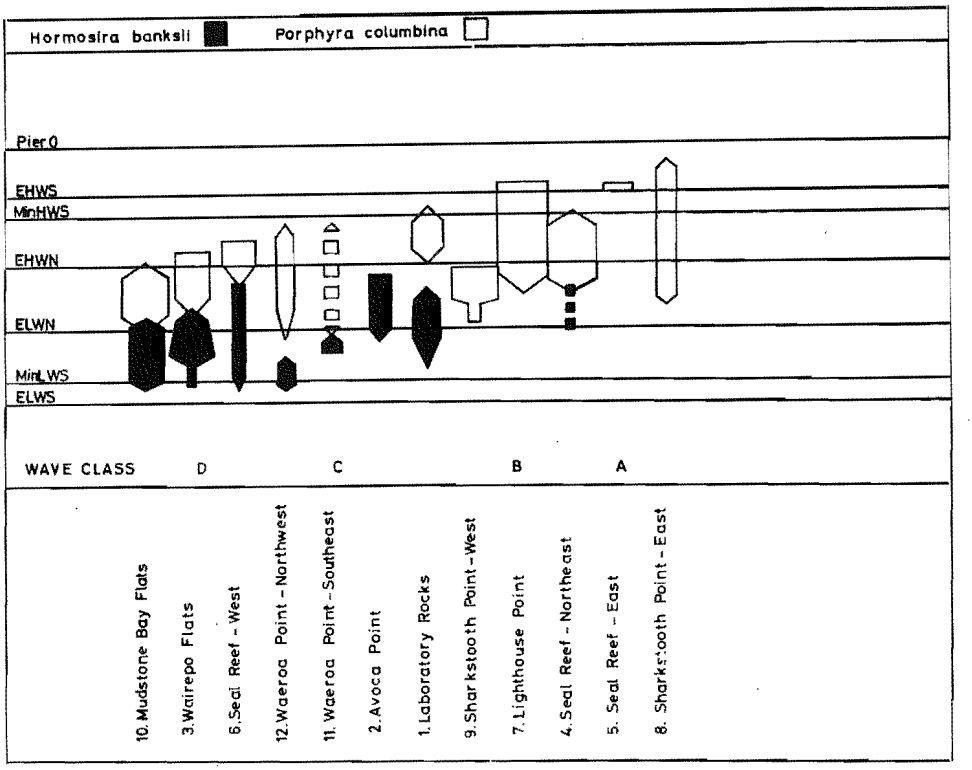
Cystophora spp.
Carpophyllum maschalocarpum
Durvillea spp.
Pier 0
EHWS
MinHWS
EHWN
ELWN
MinLWS
ELWS
WAVE CLASS
D
C
B
A
10. Mudstone Bay Flats
3. Wairepo Flats
6. Seal Reef - West
12. Waeroa Point - Northwest
11. Waeroa Point - Southeast
2. Avoca Point
1. Laboratory Rocks
9 Sharkstooth Point - West
7. Lighthouse Point
4. Seal Reef - Northeast
5. Seal Reef - East
8. Sharkstooth Point - East

Figure 25.

The vertical distribution and abundance of the dominant brown algae of the lower eulittoral: Cystophora spp., Carpophyllum maschalocarpum, and Durvillea spp. The transects are arranged in a graded series relative to wave exposure.

Figure 26.

The vertical distribution and abundance of Corallina officinalis, within the eulittoral. No distinction is made between the upright, articulated form and the prostrate form. The transects are arranged in a graded series relative to wave exposure.


Hormosira banksii
Porphyra columbina
Pier 0
EHWS
MinHWS
EHWN
ELWN
MinLWS
ELWS
WAVE CLASS
D
C
B
A
10. Mudstone Bay Flats
3. Wairepo Flats
6. Seal Reef - West
12. Waeroa Point - Northwest
11. Waeroa Point - Southeast
2. Avoca Point
1. Laboratory Rocks
9. Sharkstooth Point - West
7. Lighthouse Point
4. Seal Reef - Northeast
5. Seal Reef - East
8. Sharkstooth Point - East

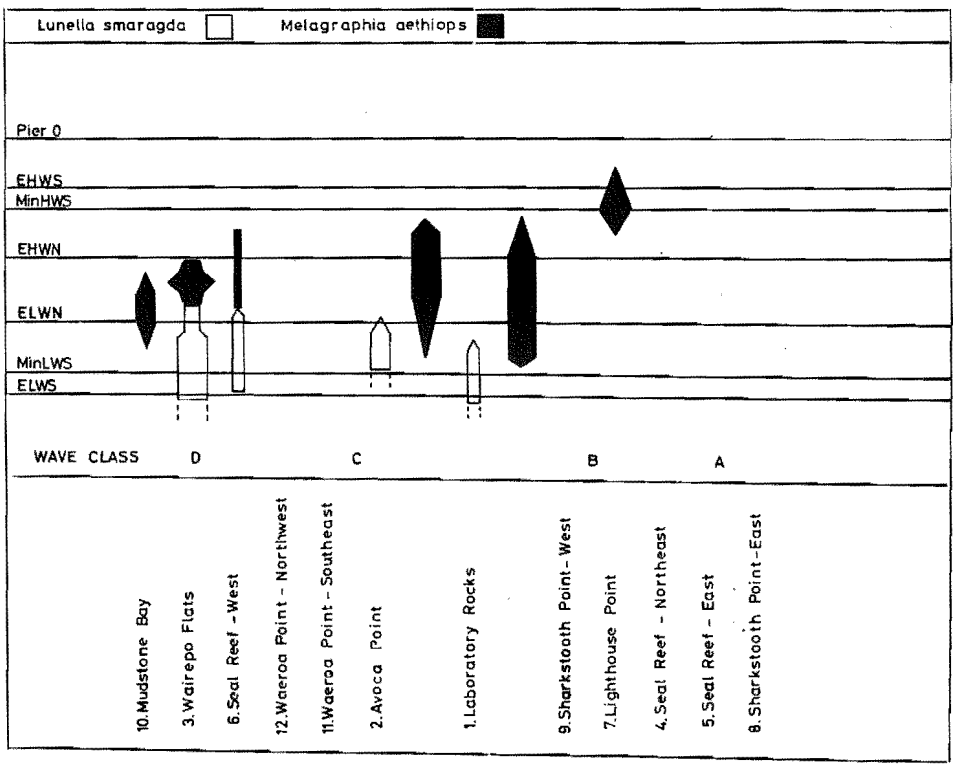

Lunella smaragda
Melagraphia aethiops
Pier 0
EHWS
MinHWS
EHWN
ELWN
MinLWS
ELWS
WAVE CLASS
D
C
B
A
10. Mudstone Bay
3. Wairepo Flats
6. Seal Reef - West
12. Waeroa Point - Northwest
11. Waeroa Point - Southeast
2. Avoca Point
1. Laboratory Rocks
9. Sharkstooth Point - West
7. Lighthouse Point
4. Seal Reef - Northeast
5. Seal Reef - East
8. Sharkstooth Point - East

Figure 27.

The vertical distribution and abundance of the dominant algae of the middle and upper eulittoral: Hormosira banksii and Porphyra columbina. Irregular distributions are indicated by breaks in the diagram. The transects are arranged in a graded series relative to wave exposure.

Figure 28.

The vertical distribution and abundance of the dominant gastropods of sheltered shores: Lunella smaragda and Melagraphia aethiops. The transects are arranged in a graded series relative to wave exposure.

Cellana spp
Pier 0
EHWS
MinHWS
EHWN
ELWN
MinLWS
ELWS
WAVE CLASS
D
C
B
A
10. Mudstone Bay Flats
3. Wairepo Flats
6. Seal Reef - West
12. Waeroa Point - Northwest
11. Waeroa Point - Southeast
2. Avoca Point
1. Laboratory Rocks
9. Sharkstooth Point - West
7. Lighthouse Point
5. Seal Reef - East
8. Sharkstooth Point - East

Chamaesipho columna
Chamaesipho brunnea
Elminius plicatus
Pier 0
EHWS
MinHWS
EHWN
ELWN
MinLWS
ELWS
WAVE CLASS
D
C
B
A
10. Mudstone Bay Flats
3. Wairepo Flats
6. Seal Reef - West
12. Waeroa Point - Northwest
11. Waeroa Point - Southeast
2. Avoca Point
1. Laboratory Rocks
9. Sharkstooth Point - West
7. Lighthouse Point
4. Seal Reef - Northeast
5. Seal Reef - East
8. Sharkstooth Point - East

Figure 29.

The vertical distribution and abundance of Cellana spp., the dominant gastropod of the eulittoral on all but the most sheltered shores. The transects are arranged in a graded series relative to wave exposure.

Figure 30.

The vertical distribution and abundance of the barnacle species: Chamaesipho brunnea, C. columna, and Elminius plicatus. The transects are arranged in a graded series relative to wave exposure.

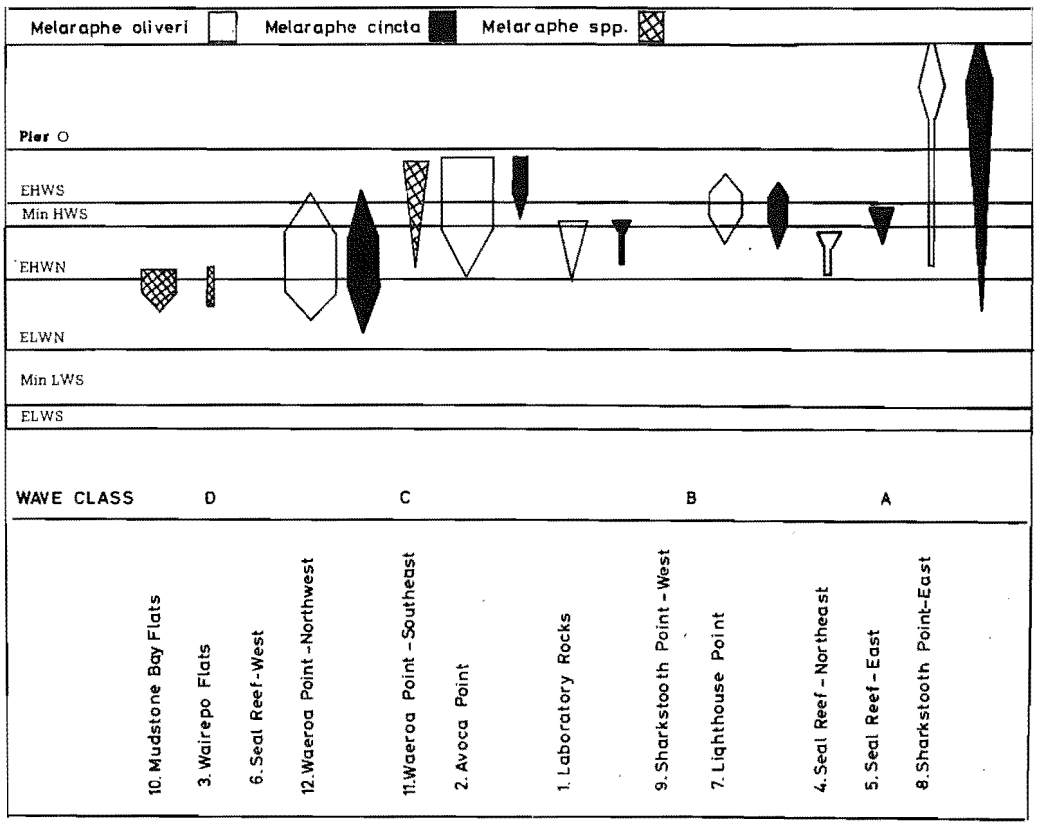

Melaraphe oliveri
Melaraphe cincta
Melaraphe spp.
Pier O
EHWS
Min HWS
EHWN
ELWN
Min LWS
ELWS
WAVE CLASS
D
C
B
A
10. Mudstone Bay Flats
3. Wairepo Flats
6. Seal Reef - West
12. Waeroa Point - Northwest
11. Waeroa Point - Southeast
2. Avoca Point
1. Laboratory Rocks
9. Sharkstooth Point - West
7. Lighthouse Point
4. Seal Reef - Northeast
5. Seal Reef - East
8. Sharkstooth Point - East

Figure 31.

The vertical distribution and abundance of Melaraphe spp., the prominent littorinids of the littoral fringe.

Interspecific Reactions as Modifying Factors of Vertical Distribution.

The number of studies dealing with the interaction of littoral species is not great. It has become characteristic of the literature of intertidal ecology to demonstrate a correlation between tide levels, and exposure, with the vertical levels of species distribution and to conclude that desiccation is a major limiting factor of vertical distribution, modified by other factors such as inter-specific competition. It is seldom that any demonstration is made of these modifying factors. Notable exceptions are to be found. Connell (1961a, 1961b) has produced an excellent series of studies on the effects of predation and of interspecific competition on the distribution of two species of English barnacles. Castenholz (1961) has provided a graphic demonstration of the grazing ability of a California littorinid. Finally, a series of studies are available on the feeding habits of limpets (Southward in Crisp 1964). While these studies help us to understand the behavior of the organism studied, they often are not directed at the problem of vertical limits.

Grazing forms

In 1963, a series of experiments were initiated with the intention of discovering and measuring such interspecific reactions that could be found to modify vertical distributional limits of the topographical dominants of the Kaikoura Peninsula, (Appendix 2). The first of these experiments dealt with the activities of grazing molluscs. Castenholz (1961) demonstrated that littorinid grazing prevented the formation of dense diatom and blue-green growths in the upper eulittoral and the littoral fringe. He also showed that apparent seasonal blooms did not coincide with the maximum growth of the diatoms but with the minimum grazing by littorinids. Field observations at Kaikoura also show short lived blooms of diatoms in the early winter (Fig. 40). These blooms often went lower on the shore than did the littorinids though the temporary effect was much the same as reported by Castenholz. It was also noted that the settlement of seasonal algae such as Porphyra columbina, Scytosiphon lomentaria and certain blue-greens could be first detected by the appearance of these species on the shells of limpets even though the species might not appear on the rocks until much later. These facts plus the intergrading distributions of Melaraphe spp. and Cellana spp. led to speculations concerning the effects of these grazers on the algae and upon each other.

The first experiment consisted of clearing a meter strip of sloping rock grazing molluscs and heavy covering algae from the top of the rock into the sublittoral. On either side of the strip, a further half meter was cleared entirely of organisms by scraping the rock and scouring it with wire brushes.

Completion of the experiment, as described, was defeated in part by the human inability to pick off all of the littorinids in the middle strip. Informal counts indicated that the rate of removal by a single worker was slightly less than the capacity of the organisms to migrate on to the strip. However, two workers, in two days, managed to clear the upper half meter plus a bit. After the strips were established they were maintained by fortnightly visits at which times the limpets and other patelloid forms were removed and notes taken on changes observed. A summary of the changes observed is represented by Figures 32 to 39. These represent each change at its peak, not necessarily at its first record.

Perhaps the most obvious interspecific reactions are those between grazers and sessile forms, algae and the barnacles. The immediate appearance of a diatom bloom confirmed earlier field observations. The conclusions of Castenholz (1961) seem to apply for Kaikoura. Later, simple experiments were tried to substantiate the above results. In every case, removal of molluscan grazers has been followed by the establishment of a diatom bloom. The intensity and duration of the blooms appeared to be related to weather conditions and the season of the year.

The extension of the upper limits of the algal turf organisms (Fig. 35) was of interest in that it demonstrated a measurable influence of grazing as a modifier of the limits imposed by desiccation.

The growth pattern of P. columbina was a spectacular demonstration of the effect of grazers on algal settlement and vertical distribution (Fig. 35).

1964 was not a "good" year for P. columbina and, as the diagram shows, there was little or no P. columbina on the controls. What it does not show, however, is that there was little or no P. columbina in the entire vicinity except for that which found optimal conditions of dampness and aspect. Further experiments are in progress to determine the possibility of extending the lower limits of P. columbina by the removal and exclusion of the grazing forms of the sheltered shores.

The penetration of the thick felty turf of the lower eulittoral by Siphonaria novae-zelandiae and Benhamina obliquata appeared to follow the pattern described by Southward (Southward in Crisp, 1964) for Patella vulgata. Once penetration had occurred, the area of feeding was slowly enlarged by grazing the edges of the turf rather than by establishing a forward movement through the turf.

The effect of grazing molluscs on the settlement of barncles was well demonstrated on this experimental strip (Fig. 38). Where the limpets were removed, the concentration of barncles was soon re-established on the barrier strips (b) and an increase in the total concentration occurred all along the lower limit of concentration (a) and (b). The lower limit was also extended. This demonstrates the effect of grazing pressure on the lower range of barncle settlement and that the normal lower limit is not pysiological but modified by biological pressures.

The upper limit of barnacle distribution falls well within the distribution of the littorinids. The effect of littorinid grazing on the establishment of a barnacle population is clearly shown (Fig. 38).

In the barrier strips (b) elimination of competition for food by other grazers and establishment of more "pasture" by removing the barncles combined to increase the density of the littorinid population. These, in turn, have made it difficult for the barncles to establish themselves in this fringe of their distribution, where survival is already threatened by desiccation. The fact that some barnacles have become established indicates that re-establishment will eventually occur. The formation of crevices suitable for settlement, by the presence of mature barnacles, combined with the gregariousness effect that causes acceleration of settlement, will outweigh the grazing pressure. The effects of substrate irregularities on barnacle settlement have been demonstrated several times by Crisp and Barnes (1954), Connell (1961), Luckens (1964) and others and were evident on this experimental strip (Pl. 24). The acceleration of settlement has been discussed by Knight-Jones (1953) and appears to have been operative here and on other experimental strips (Appendix 2).

On the more sheltered platforms, the population of limpets is very low. In places like Wairepo Flats and Mudstone Bay Flats the dominant grazing forms are M. aethiops and L. smaragda. That these have an effect upon the algae similar to that of the limpets on P. columbina and the turf formers was demonstrated in the course of experiments designed to test relationships between the plant series of the sheltered platforms. Strips of rock were cleared of the dominant alga, from the lower limit of the upper species to a point considerably lower on the shore, in an effort to extend the lower limits of the upper species.

The prime purpose of these experiments was thwarted, or delayed, by the grazing of L. smaragda and M. aethiops which drastically reduced the effective settlement and establishment of algae on these strips. In this way, it is believed that these grazers lower the efficiency of the settlement and growth of P. columbina and H. banksii near the lower edge of their ranges and possibly have a similar effect on Cystophora torulosa at the upper edge of its range.

Because of the apparent similarity of effects on the diatom population, the P. columbina settlement, the barnacle settlement, and the relative positions of the littorinids and the limpets, particular attention was paid to any indication of a competitive effect between Melaraphe spp. and Cellana spp. An immediate effect was noticed (Figs. 34 and 39) but it disappeared so quickly and had been so natural in appearance that some doubt was present as to its validity. After that, particular attention was paid to eliminating all patelloid grazers near the lower limits of the distribution of Melaraphe spp. Only occasionally were single Melaraphe found below the normal range. These were not frequent enough, nor numerous enough to be experimentally significant but they were regular enough to be tantalizing. Finally, it was noted that the concentration of another small gastropod, Risselopsis varia was disproportionately large in the experimental area (Fig. 35). Investigation of surrounding areas showed that R. varia was common at this level but nowhere as abundant as on the experiment. R. varia was then attacked with great vehemence. The removal of R. varia was immediately followed by an extension of the lower distribution of Melaraphe spp. Thereafter, it was found that the lower limit of Melaraphe spp. could be manipulated by the experimenter by the degree of control exercised upon other molluscs near its lower limits (Fig. 39). It is believed that only the unsuitability of the substrate prevented the further extension of the lower limit of Melaraphe spp. at this site. Field records and other experiments (Appendix 2) show the occasional occurance of isolated M. cincta below the normal range.

It is evident that the normal range of Melaraphe spp. is not physiologically controlled but is limited by inability to compete with more vigorous grazers.

The sequence of littorinid above limpets is the usual pattern of the semi-exposed (Class B wave action) and exposed (Class A wave action) shores. The pattern on the less exposed shores (Class C and D wave action) is littorinid above, and overlapping with, the trochid M. aethiops, which is above, and overlapping with, the turbonid, L. smaragda. Early experiments designed to test possible competitive factors between these species were frustrated by the extreme mobility of M. aethiops and L. smaragda and the lack of suitable materials for inclusion or exclusion barriers. In these localities, there is a complexity of populations that could have a total limiting effect on any one species without any one member being necessary. Thus, Melaraphe spp. are seldom found below the upper limit of the Hormosira banksii and L. smaragda. M. aethiops, in turn, tolerates the presence of L. smaragda but seldom penetrates lower than the upper range of the complex of minute gastropods and crustaceans that inhabit the lower H. banksii belt and the Cystophora torulosa band. It is suggested that the increasing complexity of populations that is encountered in descending the shore forms an increasingly hostile competitive environment in which neither food, nor space, nor proper substrate are available for organisms otherwise physiologically capable of occupying a wider range.

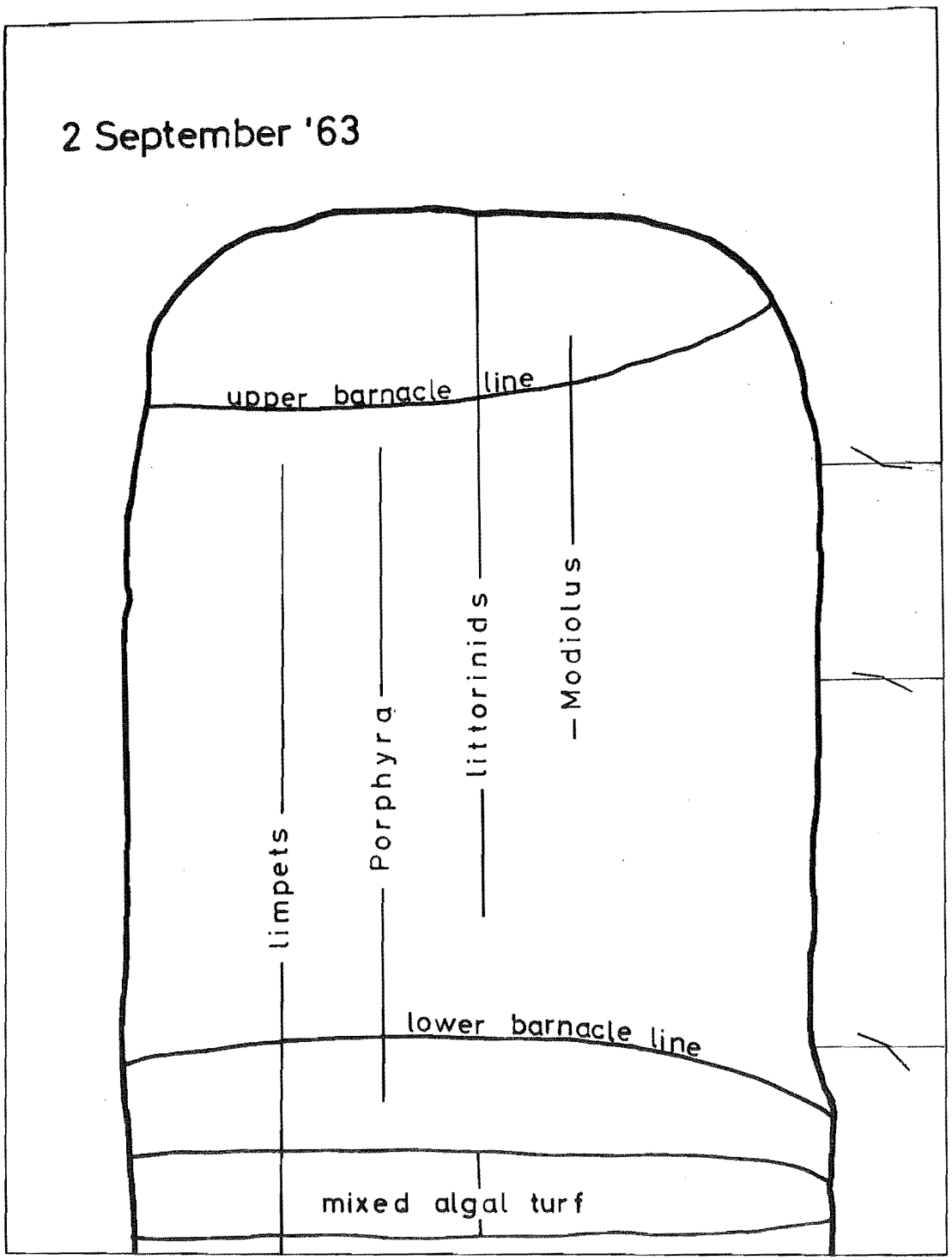

2 September '63
upper barnacle line
limpets
Porphyra
littorinids
Modiolus
lower barnacle line
mixed algal turf

Figure 32.

The condition of an experimental surface at Avoca Point on the day before the experiment commenced, 2 September 1963, indicating the levels occupied by the major groups of organisms.

Represented is a face of an isolated rock mass. The face bordered on a surge channel and was exposed to the sun from early morning until mid-afternoon. Wave action was of a fairly intense nature from the right side (facing the diagram), being in the (B) zone, cf. I. B. 3.

Lines to the right of the diagram indicate the level and degree of changes in slope.

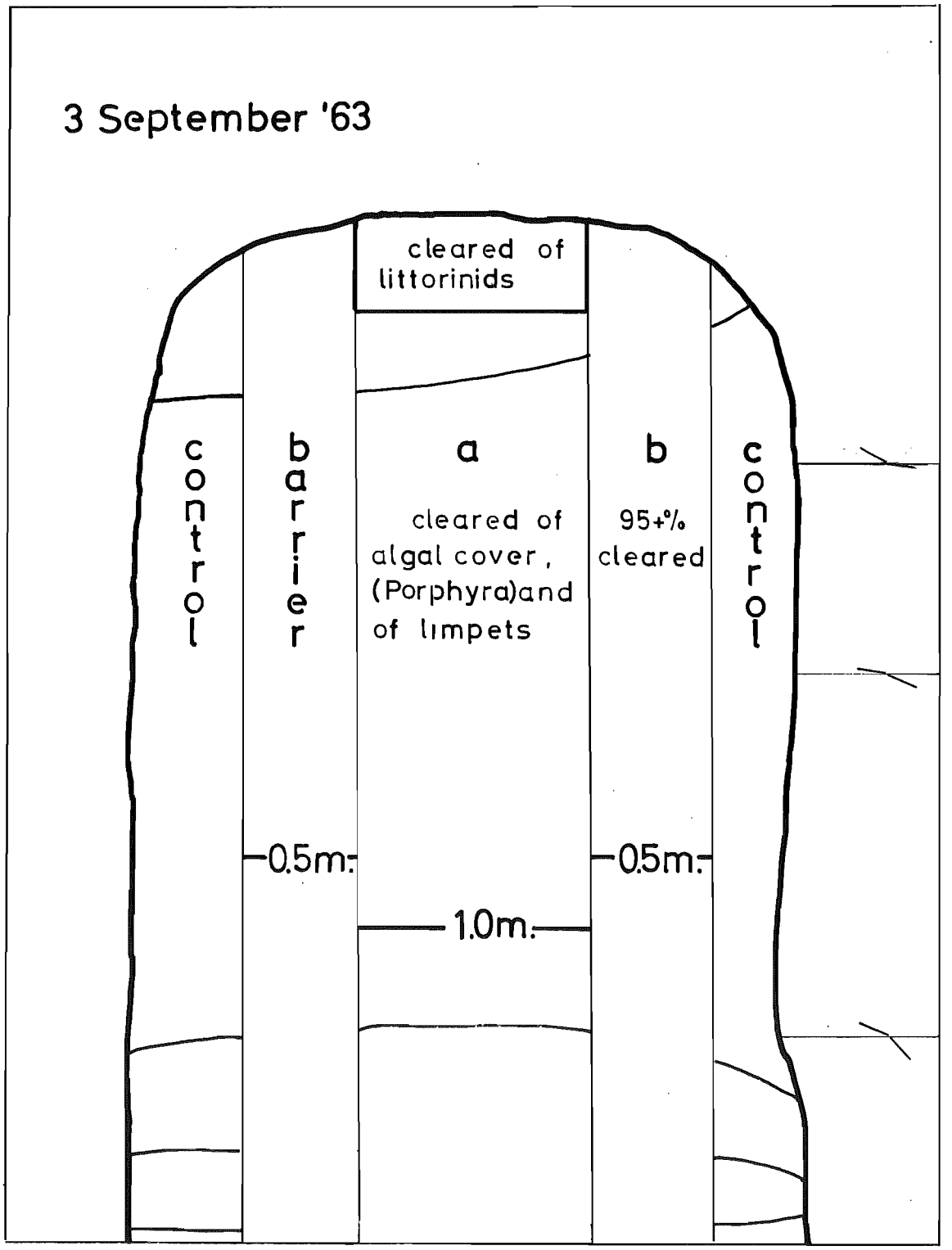

3 September '63
cleared of littorinids
control
barrier
a
cleared of algal cover, (Porphyra) and of limpets
b
95+% cleared
control
0.5m.
0.5m.
1.0m.

Figure 33.

A diagrammatic representation of the experiment. Center strip (a) was cleared completely of Porphyra columbina and limpets. Strips (b)arrier were scraped and scrubbed until at least 95% of the organisms were removed. Strips (c)ontrol were untouched. Only a small area at the top of (a) was effectively cleared of littorinids.

19 October '63

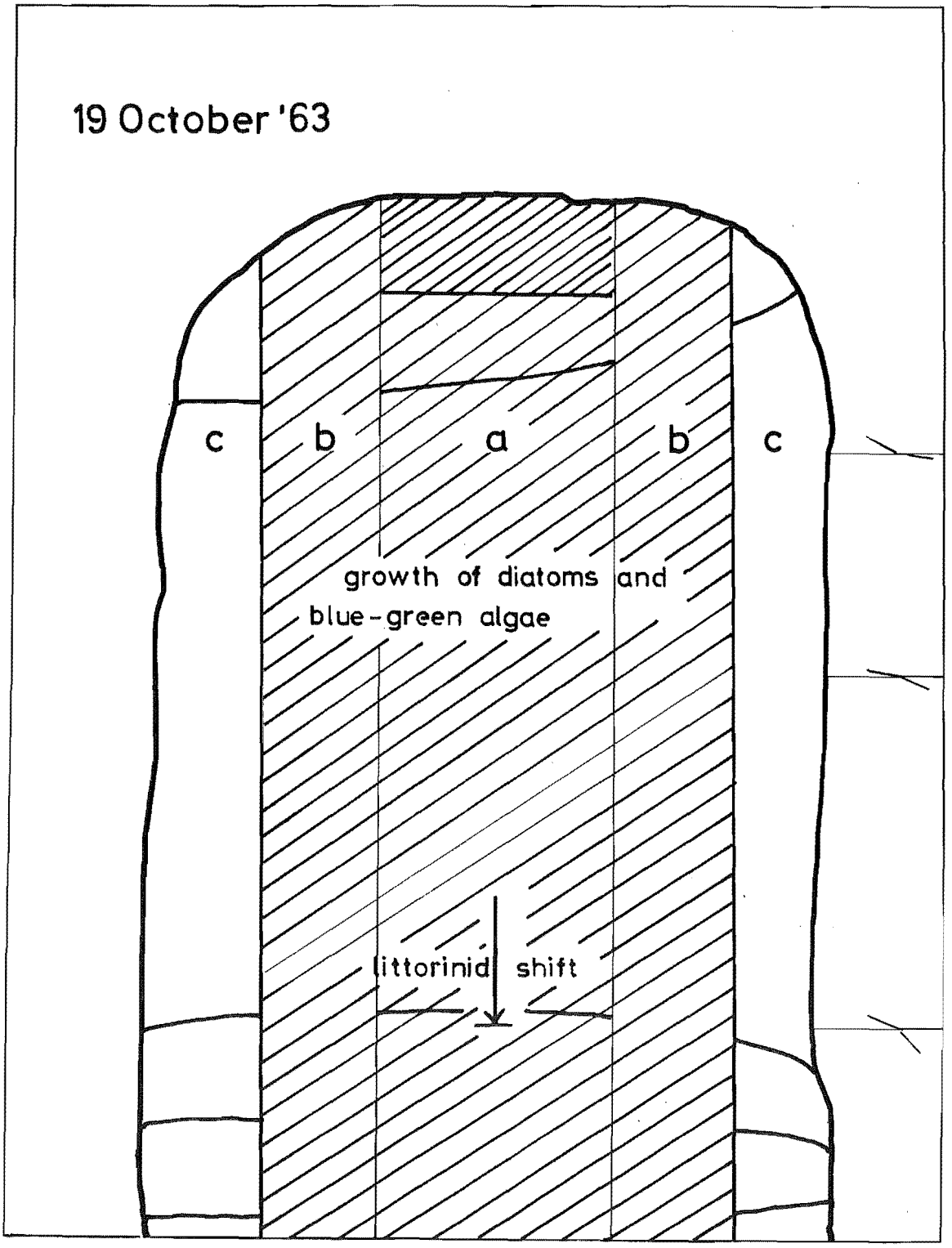


Figure 34.

Showing the condition of the experimental face on 19 October, 1964. The main reaction noted was a bloom of diatoms and blue-green algae and a shift in the lower concentration of littorinids of Melaraphe spp. Other reactions had begun but they are recorded only at their peak, in order to more clearly demonstrate the time required for a complete reaction.

12 February '64

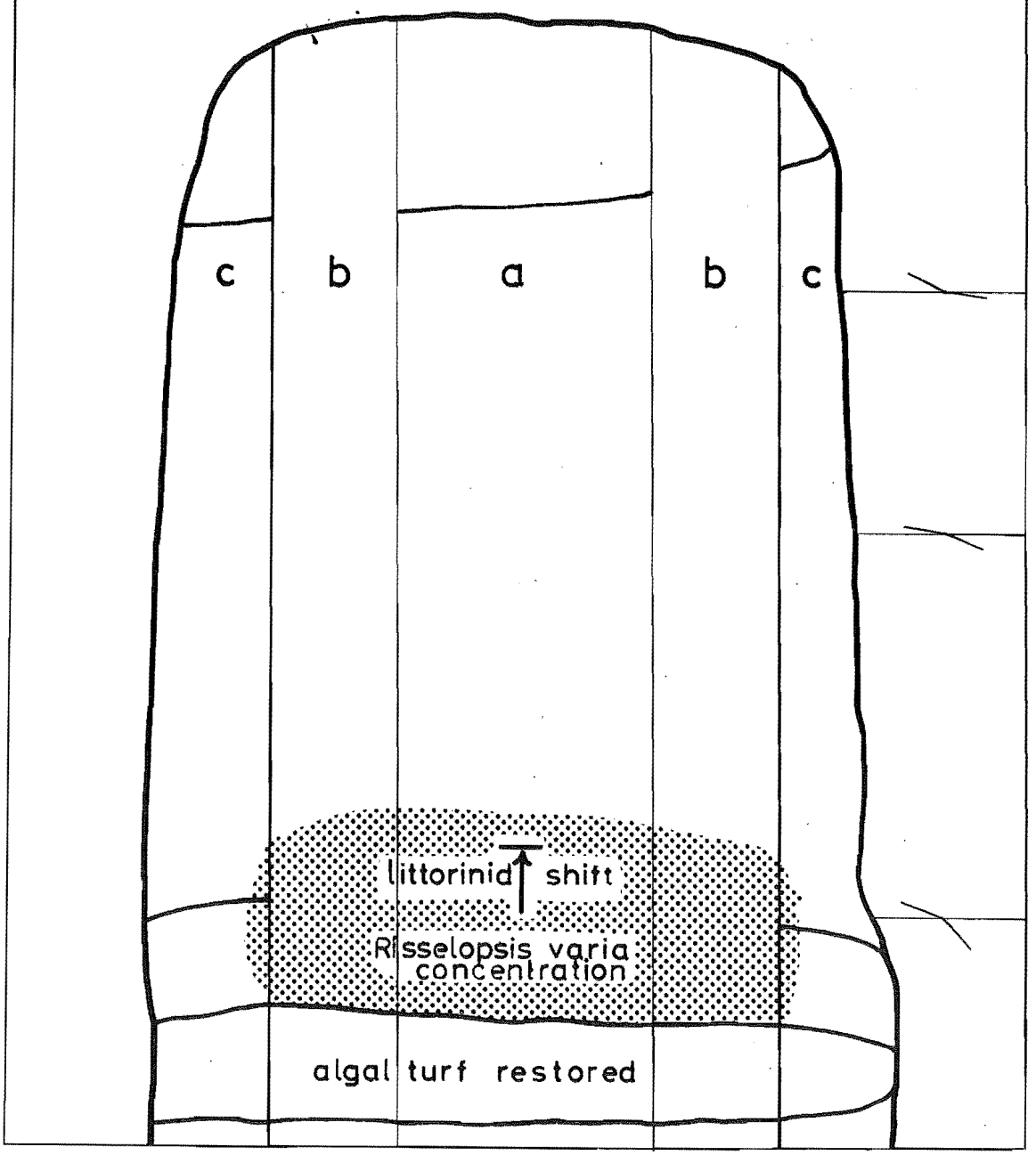


Figure 35.

Illustrating the reversal of the downward shift of Melaraphe spp. The increased concentration of Risselopsis varia was at first overlooked because of the inconspicuous appearance of the animal and because it was not expected.

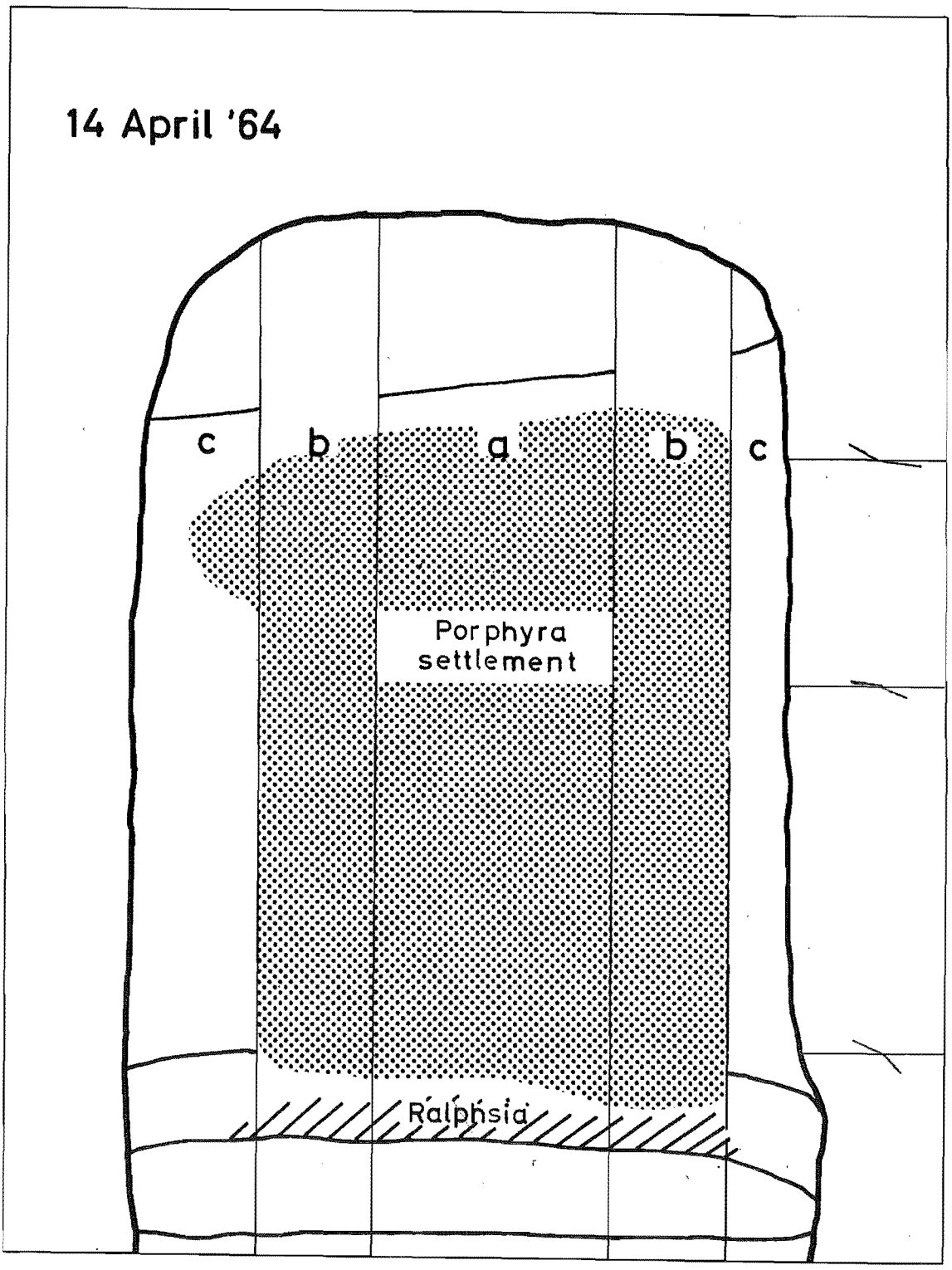

14 April '64
c
b
a
b
c
Porphyra
settlement
Ralphsia

Figure 36.

The establishment of a heavy cover of Porphyra columbina on the experimental strip was perhaps the most striking reaction of the experiment because it was so complete and so visible. The small pocket of P. columbina on the upper left control occurred in a damp pocket in the rock. Similar patches occurring on other rocks were the only other signs of this seaweed in the immediate vicinity.

The line of Ralphsia verrucosa that appeared was also quite unexpected as this plant is normally confined to shaded areas.

16 June '64

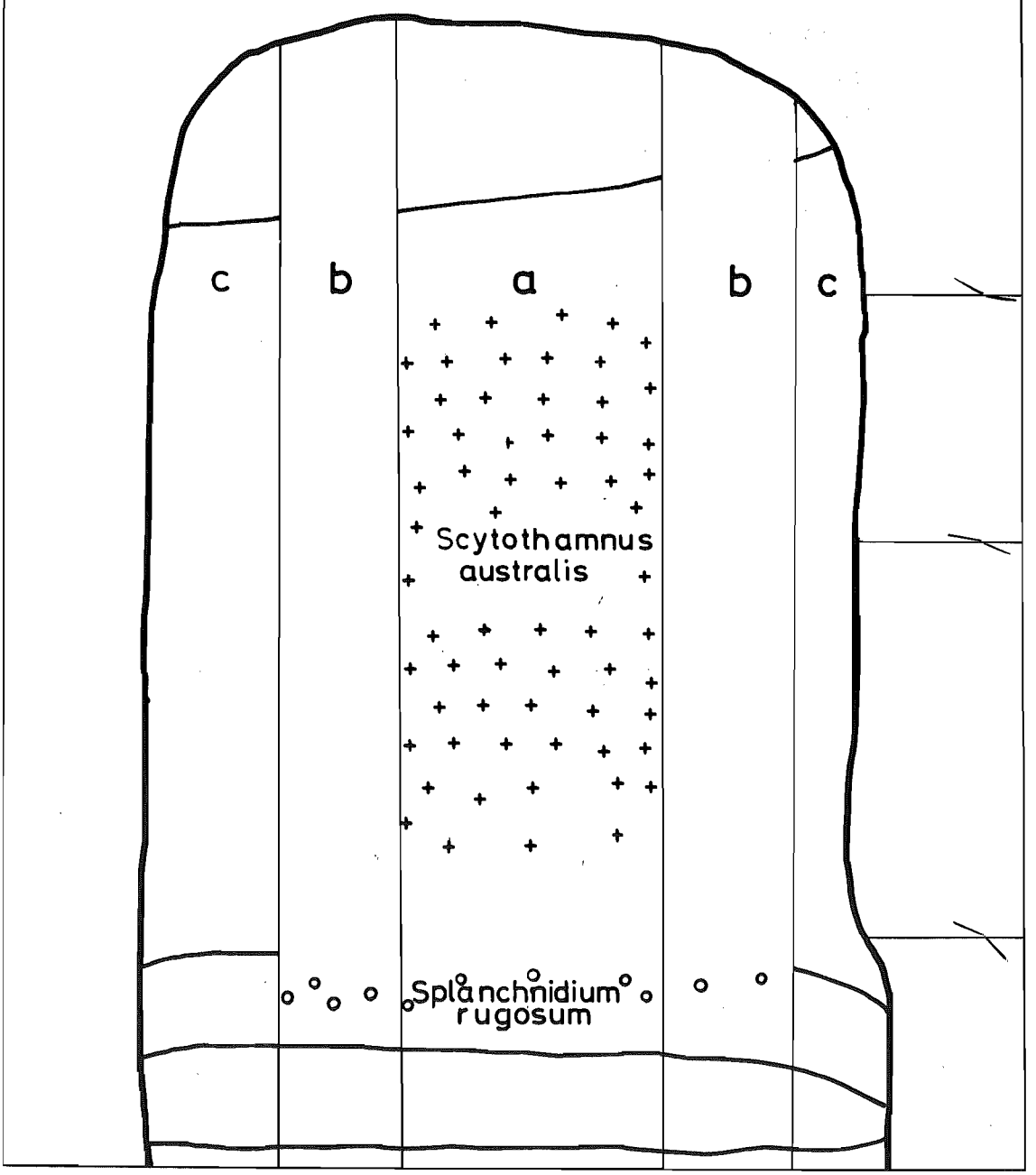


Figure 37.

Scytothamnus australis appeared under the cover of Porphyra columbina. The distribution was scattered and was limited to the barnacle covered area. The plants were never large. They persisted after the Porphyra columbina was removed but appeared to suffer some desiccation damage.

A small number of Splanchnidium rugosum plants are a common feature in this and similar areas but the growth indicated here was exceptionally heavy and long lasting.

23 December '64

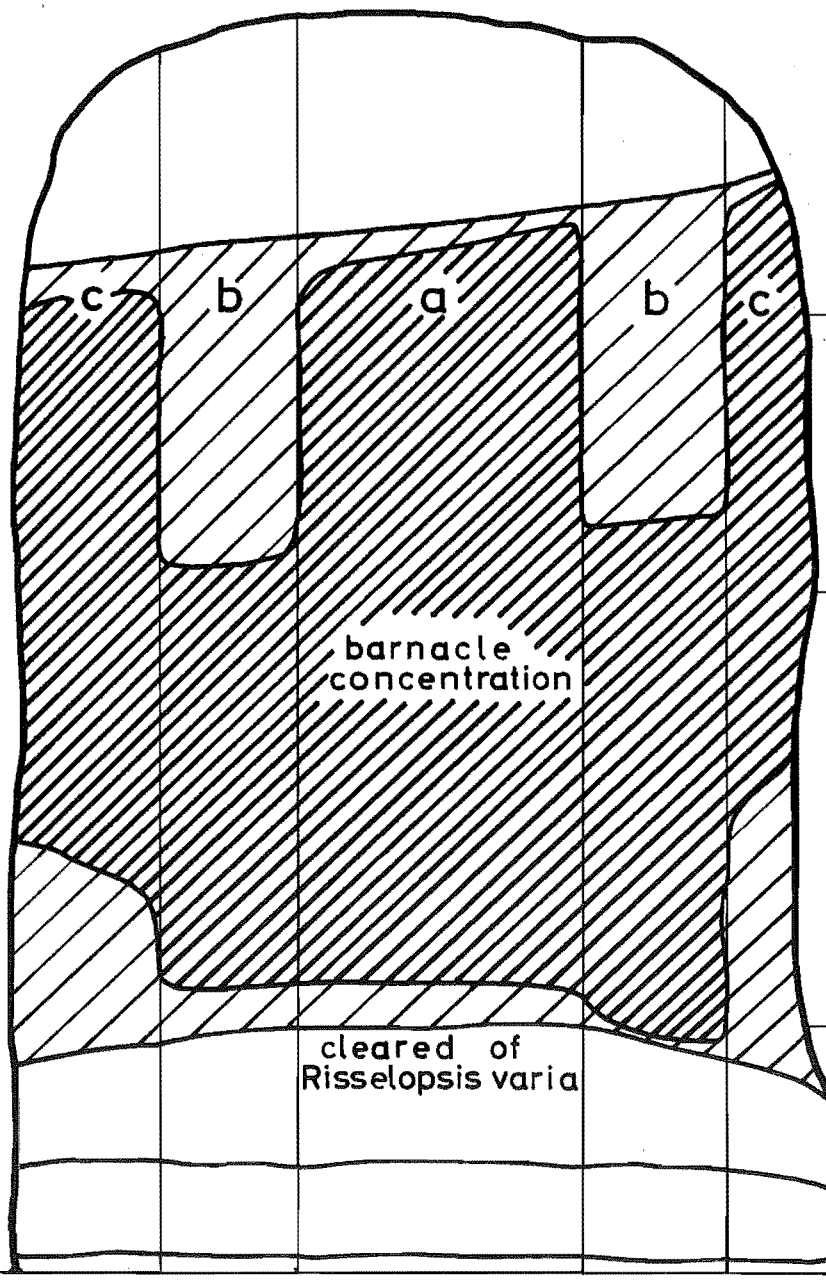


Figure 38.

Barnacle settlement was fairly constant from the beginning of the experiment but the pattern being established was not clear until nearly a year after the experiment began. Almost all of the re-settlement was due to Chamaesipho columna. Although Elminius plicatus occurred in the original population, very little new settlement of this species was noted.

The low concentration of settlement in the upper portions of the barrier strips is believed to be due to littorinid grazing.

At this time, Risselopsis varia was removed from (a) and (b).

9 January '65

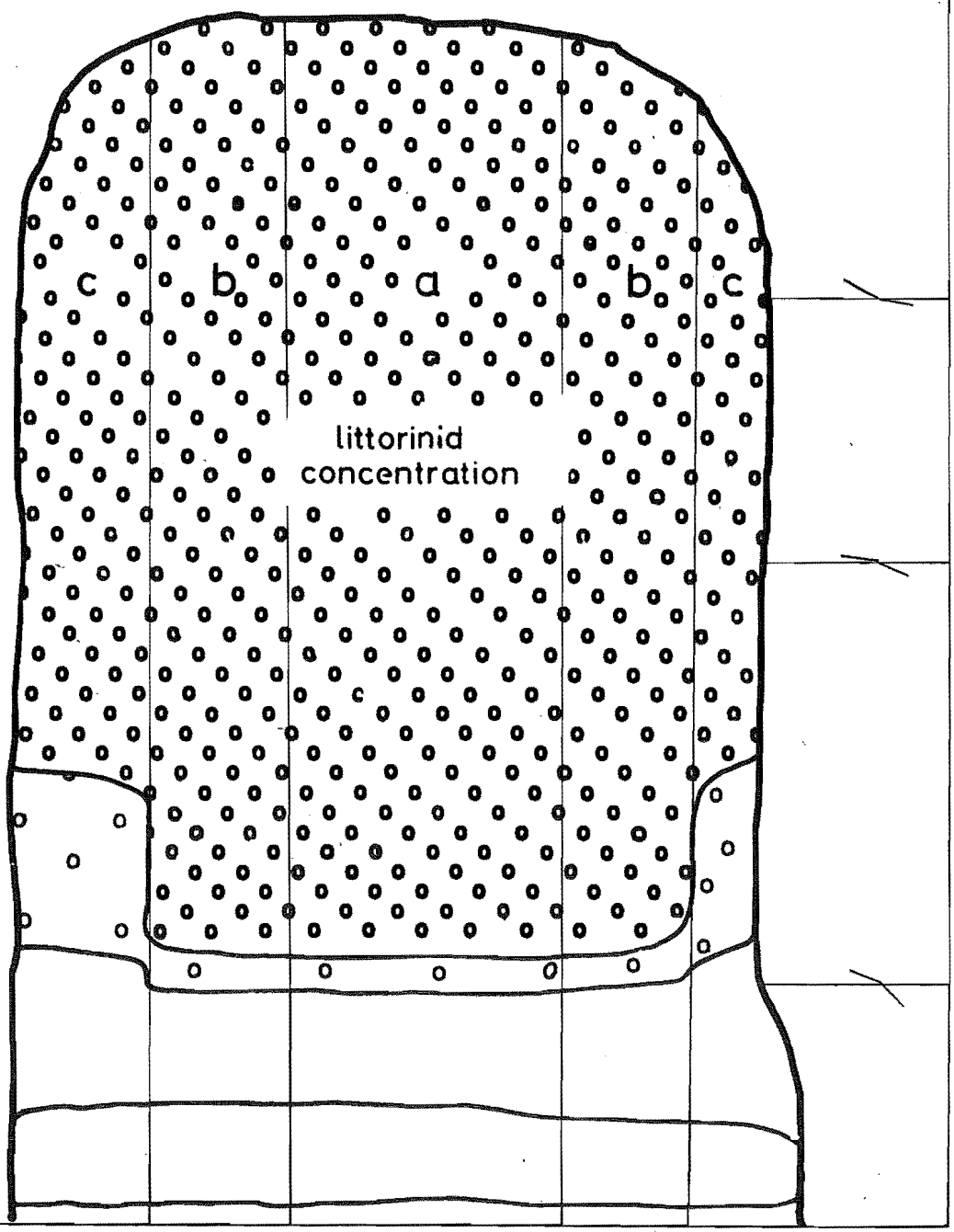


Figure 39.

This illustrates the almost immediate effect of removing the appropriate competitor (in this case, Risselopsis varia) from the lower part of the littorinid distribution. This reaction could be repeated, at will, by allowing the R. varia concentration to increase forcing the littorinids back up the slope.

Sessile Organisms

No investigation was made of the possible reactions between the various species of barnacles or of any other sessile animals. Another study is currently in progress that will deal with barnacle distributions on New Zealand shores.

There are however, series of algal species forming vertical sequences upon the shore that lend themselves to experimentation. The most obvious of these is the Porphyra columbina, Hormosira banksii, Cystophora torulosa sequence of the sheltered shores. Field observations show that P. columbina reaches a lower limit in those areas where H. banksii is absent and that its lower limit coincides with the upper limit of the H. banksii where it is present. This indicates that the H. banksii is the successful competitor for space within the common physiological limits of both species. This is not surprising as H. banksii is present for the entire year, it is a heavy coarse form, and it grows in thick mats that occupy most of the available space. Its year around presence alone would give it a tremendous advantage over the seasonal P. columbina. Its heavy coarse structure acts mechanically to sweep the bare rock nearby. This action could, and probably does, account for the narrow band of bare rock found between the H. banksii and the P. columbina. The width of this band almost always corresponds to the length of the nearby H. banksii.

To test the hypothesis that H. banksii formed a physical barrier to the settlement and development of P. columbina a number of areas were cleared of H. banksii (Pls. 19,20). Some were scoured to bare rock, others had only the H. banksii removed. Very little grew on any of these strips for a year.

Some fresh H. banksii growth was noted in the Spring and Autumn and a goodly amount of C. sinuosa occurred on the strips that still had a C. officinalis base. At first, this failure was attributed to a belief that the strips had been established too late in the season. However, experience with the other strips used to test the effects of grazers, and the slowness with which the H. banksii recovered, even after apparent heavy settlement, indicated that molluscan grazing might be responsible. Large numbers of M. aethiops and L. smaragda were found on and near these experiments at various times. A fenced strip was then established for the following season and is presently under observation (Pl. 21).

To test the hypothesis that C. torulosa competes with H. banksii for space in the lower reaches of the range of H. banksii similar strips were prepared. The vertical overlap of these two species is not great but the almost nonexistent slope of the Wairepo Flats platform extends the actual horizontal distance of overlap to several meters. In this area there is a complete continuum from 100% H. banksii, through a mixture with C. torulosa in which the amount of H. banksii diminishes and the C. torulosa increases to 100%. The C. torulosa was removed from a strip that extended through the entire overlap of ranges (Pl. 22). This strip was maintained by periodic cleaning of the new growth of C. torulosa. In the course of this maintenance it was noted that: (1) C. torulosa and H. banksii showed nearly equal rates of settlement but that H. banksii settlement occurred to be heavy in Spring and Autumn (Pl. 23). (2) That C. torulosa settled more effectively in sediment deposits trapped by

C. officinalis whereas H. banksii settled best in cracks, pockets, and fairly clean clumps of C. officinalis. (3) That C. torulosa survived better and grew faster at the bottom of the overlap area and did less well than H. banksii at the top.

The diminishing growth rate exhibited by H. banksii near its lowest occurrence indicated that a physiological limit was being approached. This is in accord with the conclusions of Trevarthen (1954) who reported that the need for light was the lower limiting factor of H. banksii in the areas that he studied. It appeared that H. banksii could be encouraged, and a higher concentration established in the lower part of its range, but that its lower limit could not be extended any appreciable amount. Therefore C. torulosa as a competitor for space only affected the concentration and not the lower limit. It also appeared that C. torulosa was reaching a physiological limit due to desiccation at its upper limit and was not totally limited by H. banksii.

Discussion

It is pertinent, at this point, to discuss the many factors that influence zonation by summarizing the information gained about each of the topographically dominant species or species groups. As stated earlier, these are the littorinids, Melaraphe cincta and M. oliveri, the barnacles, Chamaesipho brunnea, C. columna and Elminius plicatus, the limpets, mainly Cellana spp., the trochid, Melagraphia aethiops, the turbonid, Lunella smaragda, the red alga, Porphyra columbina, and the brown algae, Hormosira banksii and Cystophora torulosa.

i. Melaraphe spp. represent the highest macroscopic organisms of the foreshore. While certain differences may be observed in the distribution of the two species, M. cincta and M. oliveri, on some shores (Knox 1953) Batham (1956, 1958), the two are found so constantly together at Kaikoura that they have been largely treated as a single ecological entity. Figure 46 summarizes their local range of distribution and the information about that range gained by observation and experiment.

The upper limit is labelled desiccation or starvation on very general principles. The truncation of substrate at Kaikoura did not allow for all of the observational information desired.

The laboratory experiments and information from other sources indicated that Melaraphe spp. will tolerate long periods of desiccation, even longer than received at the natural upper boundary. However, above the natural limit there would be a severe decrease in the wetting. In most places it drops to zero.

Perhaps, more important are the indirect effects of emergence. Above this natural limit there would be no spray or splash to supply detritus or to support the diatom populations. These are the apparent food supply of the littorinids. Further, it is necessary for the animal to move to feed. Even at their normal limits, it is difficult to determine when they can find time to come out of their protective posture long enough to feed.

It has been casually suggested that there is a definite trend for the littorinids to move up the shore whenever the opportunity offers and that the individuals at the top of the distribution have already moved out the survival and breeding range. This implies that the population is continually moving upward and dying off at the top while being replenished in the lower part of the range. The only evidence that supports this theory, to date, is the behavior of the animals in aquaria. This "conveyor belt" concept could provide some interesting possibilities for further investigation.

In any case, it seems evident that Melaraphe spp. have reached an upper limit that presents only the alternate possibilities of desiccation or starvation.

Two lines have been drawn to show possible lower limits for the vertical distribution of Melaraphe spp. The lowest is a querulous "physiological limit". It represents a continuation of the submergence level comparable to that experienced by the lowest individuals found in the field. These rare individuals were always found on Wairepo Flats, an extremely sheltered location. Submergence experiments indicate that this might be even lower, if indeed such a limit exists.

Lysaght (1941) describes a situation where an ecologically similar species, Littorina neritoides, was found in a situation that was permanently submerged for twelve months.

The second lower limit indicated represents the levels at which isolated individuals have been found, or to which the population has been extended in field experiments. In the sheltered situations the range has been very limited. This limit coincides with the upper boundary of a heavy and complex plant cover and an attendant small-animal population. It is postulated that the environment becomes totally unsuitable, biologically though not physically.

In the areas of intermediate wave action the natural lower limit was somewhat above this total plant cover. Experimentally, it was possible to extend this population by removing competitors (Figs. 34 and 39). In the most wave exposed areas the rock faces did not afford sufficient protected pits and cracks, etc. as was evidenced by finding the population extending much lower at the very most exposed face. Here there were fine cracks in the rock and numbers of crevices between barnacles. These were occupied by littorinids.

The concentration of the population decreases in the exposed places as indicated by the shading of the diagram. This effect, and the size distribution effect illustrated on Figure 20, lead to speculations about the biology of Melaraphe spp. that could also lead to interesting studies. Castenholz (1961) reported a similar effect among littorinids on the Oregon coasts and attributed the ability of the smaller individuals to survive more wave action to a volume/attachment area relationship.

The relationship of size of individuals to severity of environment might also indicate that a higher growth rate is maintained throughout the life span because of the extended feeding time available.

ii. Porphyra columbina occupies the highest inter-tidal range among the macroscopic algae common on the peninsula and is second only to the littorinids among the topographic dominants.

Figure 45 illustrates the apparent simplicity of its distribution. The levelling of the desiccation limit in the more exposed areas is due to the change of slope at this level. The rock tops flatten and the splash and spray do not carry as far vertically as they do, or would, if the steeper slopes continued upward.

The large "bite" out of the lower distribution corresponds exactly with the upper distribution of Hormosira banksii. There is, in fact, no place left for P. columbina to attach in this area. The slight raising of the limit in more exposed areas is largely speculative being indicated only by the existence of isolated plants and clumps of plants at a level corresponding to the lower line. No label has been given the lower line because, as of yet, no indication has been available from observation, experiment, or the literature concerning the lower limit of P. columbina.

Data is still being sought from field experiments to confirm this level.

iii. Barnacles have largely been excluded from this study. There is an extensive study in progress on New Zealand barnacles and an abundant literature on English and American barnacles.

Studies on English barnacles by Connell (1961a, 1961b) and by many others, a study of tide factors in a Norwegian fjord (Brattegard and Lewis 1964), and personal observations indicate that emergence factors cause the upper distributional limits of the barnacles. Desiccation of cyprids and young barnacles seems to be the major limitation.

Interspecific reactions cause a sorting of two forms into separate bands on English shores (Connell 1961a). A similar effect is noted here though it is not always as clear cut as on the English shores. Settlement preferences for crevices and other declevities have been reported and are very evident in Chamaesipho columna at Kaikoura (Pl. 24.).

Lower limits may be due to substrate selection by cyprids or to predation.

iv. Melagraphia aethiops is one of the most abundant species on the Kaikoura Peninsula. It exists in high concentrations on all of the extended siltstone platforms where the nearly level aspect prevents wave shock. Its range is overlapped by the lower distribution of Melaraphe spp., by the upper distribution of Lunella smaragda (particularly in winter) and laterally by the limpets, Cellana spp. in the areas of intermediate wave action. Figure 44 summarizes its distribution and the factors that appear to influence the distribution. The large gap in distribution does not indicate that the species was entirely absent but that the concentration was low and irregular on the transects covering that range. Because of this discontinuity and irregularity it was not possible to determine vertical limits satisfactorily. Lack of suitable substrate appears to account for this gap.

It may be noted that there is a variance in the boldness in the lettering used to label various factors on these diagrams (Figs. 41-46). The boldness of the label indicates the relative importance of the factor or the degree of certainty of the author. The upper limit is ascribed to desiccation or starvation. This is in line with the performance of M. aethiops in the desiccation experiments performed at Kaikoura and with the observations and conclusions of Clark (1957) who examined this species on a New Zealand boulder beach. M. aethiops does not tolerate desiccation well (Appendix 2). It is also a much larger organism than the Melaraphe spp. in and above its range. It may be that its food requirements are so great that it needs more feeding time and cannot compete with the more efficient littorinids. Littorinid competition is strongly indicated by the field observations at the more wave exposed sites.

The lower limit is ascribed to settlement conditions on the basis of the size class distribution (Fig. 22) and on the observations of Clark (1957). It appears that the larvae are distributed throughout a wide intertidal range but not below low water. The first year mortality is very high at both ends of the vertical distribution and the survivors are concentrated in a very narrow range. As the individuals get larger they are better able to compete, survive predation, and survive desiccation and a migration in both directions extends the range somewhat. A raising of the lower limit by competition with Lunella smaragda is noted in the sheltered areas. It is far from certain how this effect comes about. Gut analysis were not particularly rewarding.

Most of the contents were the "pablum" of ground rock particles mentioned by Clark. Better results were obtained with L. smaragda. The few diatom valves found in both indicate that there may be enough similarity in diet to make food competition a factor. It is obvious that the upper M. aethiops feed on diatoms and detritus, as there is nothing else available (considering spores, protonema, etc. as detritus because they are outside their survival range). However, L. smaragda does ingest larger particulate matter. On strips cleared for algal competition experiments both species occurred in abundance for some time, grazing the bare rock. Eventually the M. aethiops moved up and out leaving Lunella as the only likely competitior on the strips.

Evidence for a lateral limitation by wave action is abundant in the field. M. aethiops does not adhere strongly to the substrate when in its protective posture. It could easily be washed off of smooth sloping surfaces. In fact, in wave washed areas, it is found only where there is some protection, as in gullys and on ledges. It is also possible that there is considerable competition pressure from the limpets in the areas of intermediate wave action as indicated by a lessening of M. aethiops concentration where the two forms overlap in range.

v. Cellana spp. are the main elements of the limpet population at Kaikoura. Other patelloid gastropods are present in specialized habitats. An extensive study is currently being done on the Cellana spp. on these and other shores. The studies of Cellana spp. and of other patelloids in this paper have largely been confined to their activities as competitors of other dominant species.

It has been observed that the mature Cellana spp. do not tolerate constant submergence (Mannering pers. comm.), at least in still waters. This has been observed in related English species (Southward, in Crisp, 1964) and partly accounted for by a need to keep the gills free of clogging.

That the food supply of the limpets consists of diatoms, algal sporelings, and animal sprat is indicated by the growth of these organisms on experimental strips after the removal of the limpets. In particular they have been observed to affect the establishment of Porphyra columbina, and Scytothamnus australis (Figs. 36 & 37), the lower limits of littorinids (Figs. 34 & 39), barnacle settlement (Fig. 38), and the diatom bloom (Fig. 34).

It seems likely that the upper limit of the limpet species may largely be determined by desiccation and feeding factors.

vi. Hormosira banksii is perhaps the most obvious plant on the peninsula. It forms massive carpets on the sheltered platforms. Figure 43 depicts the distribution and the modifying factors of the distribution of this fucoid. Other ecological studies have contributed greatly to the knowledge of Hormosira banksii. Trevarthen (1954) established that the upper limit of H. banksii was largely due to desiccation and that the lower limiting factor was lack of proper light. That these conclusions are valid is indicated by the field observations of this study. However, a slight grazing effect upon the sporelings in the upper reaches of the distribution was noted. It was not ascertained whether these plants would have survived future desiccation but the reduction in numbers of individuals reduces the chances of establishing

adult plants.

A definite competition effect was noted and tested at the bottom of the distribution. Here, it was shown that Cystophora torulosa competes with H. banksii for space and light and that L. smaragda grazes upon the settled spores and sporelings. It is doubtful that these effects actually raise the lower limit more than a few centimeters but they certainly affect the concentration. The inability of H. banksii to establish in wave beaten areas is obvious. This was also noted by Trevarthen (1954), who suggests that the weakness of the attachment of H. banksii may be aggravated by physical damage caused by limpets.

vii. Lunella smaragda is the largest and most mobile mollusc of the eulittoral platforms. Members of three year classes are common on sheltered shores (Fig. 23). Distribution by size classes indicates that the smallest individuals are found highest on the shore and that the largest are found only in the sublittoral. Specimens representing age groups beyond the third year appear to be entirely sublittoral.

Figure 42 depicts the intertidal range of L. smaragda on the Kaikoura shores. A highly speculative desiccation limit has been indicated. The position of this limit was abitrarily placed, being placed above that of Melagraphia aethiops (Fig. 44) and below that of Melaraphe spp. (Fig. 46) according to the results of the desiccation experiments performed in the laboratory.

The actual upper limit was observed to coincide with the upper limit of macroscopic algal cover. On the sheltered shores where the upper limit of Hormosira banksii is

congruent with the lower limit of the seasonal Porphyra columbina, a seasonal shift in the range of L. smaragda was noted. This shift did not occur in the less sheltered areas where a band free of macroscopic plants occurs below the P. columbina.

A gut analysis was attempted. The results were not particularly gratifying, at the time. Most of the gut content was a fine mush of organic material and siltstone grit. This indicated that L. smaragda does graze rock surfaces. Also noted were: diatom valves, algal protonema, cells resembling P. columbina, Colpomenia sinuosa fragments, some small red algal filaments, and one zoea. Luckens (1964) reported observation of L. smaragda ingesting Corallina and Trevarthen (1954) suggests that they nibble on Hormosira. L. smaragda are commonly found creeping over fronds of H. banksii and Cystophora torulosa. It is not possible to say if they eat these plants, graze on the epipytes of these plants, or just crawl over them when they find the plant in their path.

Placing together the facts that L. smaragda is a large active animal with a probable high food requirement, that the distribution is limited to areas with macroscopic algae, that many algal forms appear to be ingested, and that the largest animals, though more resistant to desiccation, are found lowest on the shore, indicates that the total distribution pattern and the distribution of size classes are both limited by need for an adequate food supply.

viii. Cystophora torulosa is the last topographic dominant to be considered. It occupies the lowest position on the shore.

Figure 41 summarizes its distribution. Here is the only case that I have reported of an organism extending above its desiccation limit, though it is an effect common to "understroy" flora. Certain areas were cleared of all large Hormosira and Cystophora within their range overlap. The intention was to measure relative growth rates of the smaller plants left on the strips. The C. torulosa did not grow, and often showed discoloration indicative of desiccation damage.

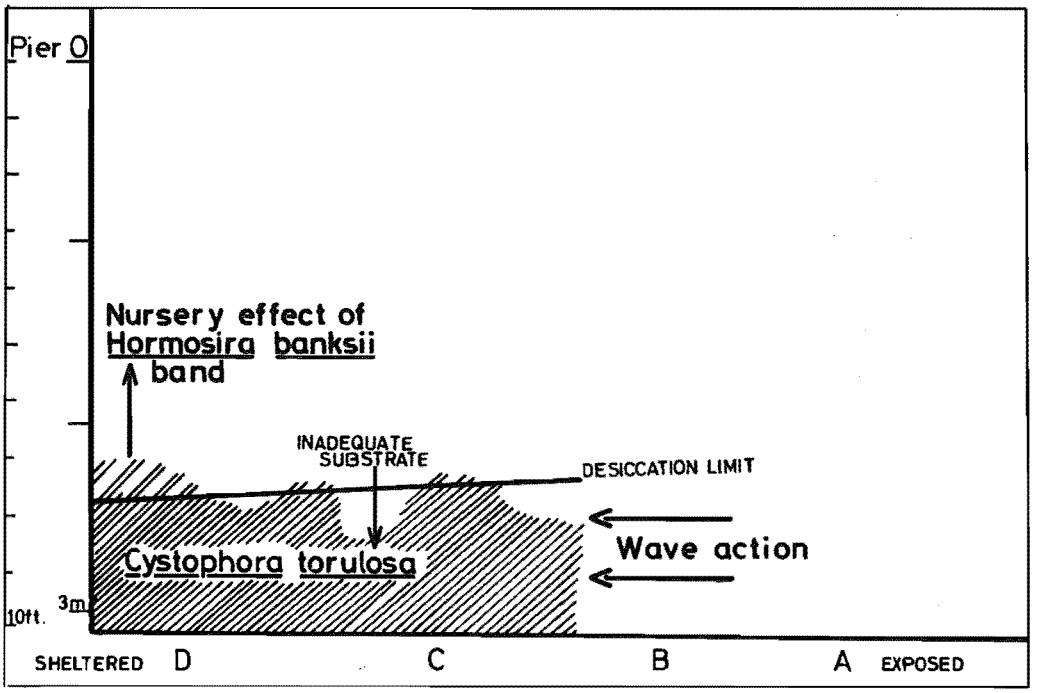
The lower limit of C. torulosa was not determined. It extends, in some cases, a few feet below the low water line. Generally, it is gradually replaced, near the low water line, by Cystophora scalaris and C. retroflexa. These near relatives have ranges that overlap for the most part. The upper limits are separated by only a few inches, vertically. The centers of distribution appear to be more disparate. The center of distribution of C. scalaris is probably below the lower limit of C. torulosa and the center of distribution of C. retroflexa is below that of C. scalaris.

ix. The upper limits of seven, of the eight, topographic dominants considered were found to be caused by physical emergence factors. In limited areas modifications of these limits by biological was observed. These modifications were minor. In the eighth case, Lunella smaragda, it was found that the upper limit was due to biological pressures. L. smaragda is an inhabitant of the upper sublittoral and the lower eulittoral.

The lower limit of one alga, Hormosira banksii, has been shown to be due to a submergence factor, lack of adequate light. It seems probable that the lower limits of the other algae considered may be largely due to this factor.

Slight modifications of their lower limits can be attributed to biological pressures. Of the animal species considered, only Cellana spp. appeared to have lower limits determined by physical factors of submergence. Melaraphia aethiops and Melaraphe spp. appear to be limited by biological pressures.

These findings are consistent with the findings of other workers, in other places, working on similar plants and animals. A pattern has appeared that is similar to that which we expect in other environments where a graduated increase in climatic severity is found, such as deserts, high latitudes, high altitudes. Where the environment is most harsh, as in the littoral fringe, the number of species is low and the population limits are largely physical. As the environment becomes less harsh, the number of species increases and the population limits become largely due to interspecific pressures and the complexity of the interaction of pressures increases.


Pier 0
Nursery effect of
Hormosira banksii
band
INADEQUATE
SUBSTRATE
DESICCATION LIMIT
Wave action
Cystophora torulosa
10ft.
3m
SHELTERED
D
C
B
A
EXPOSED

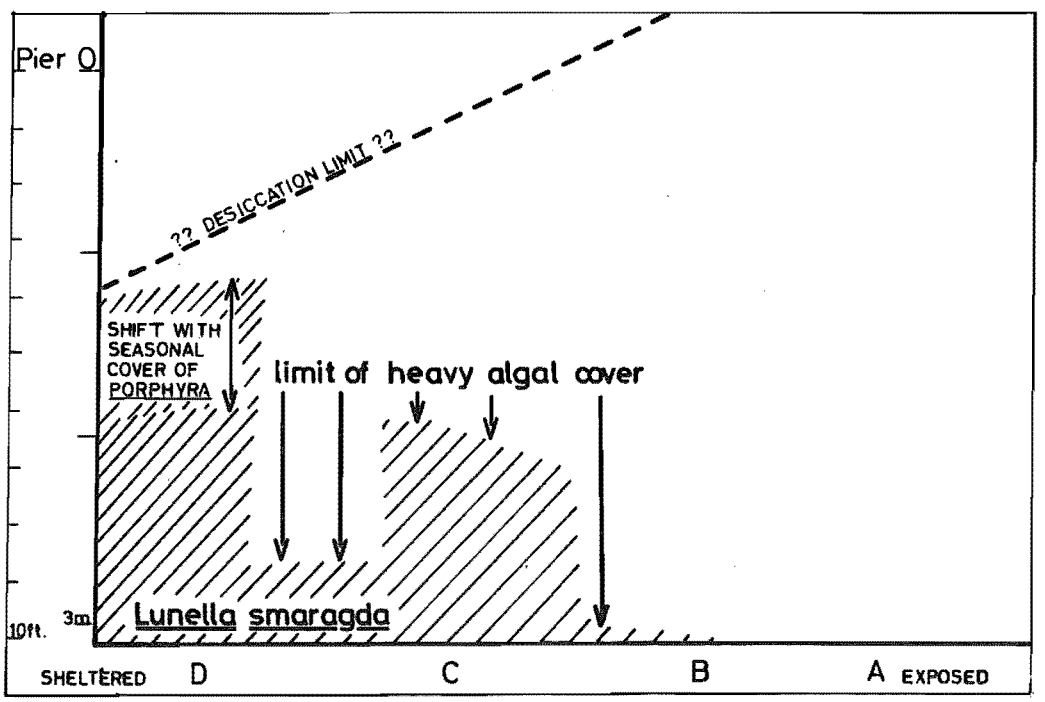
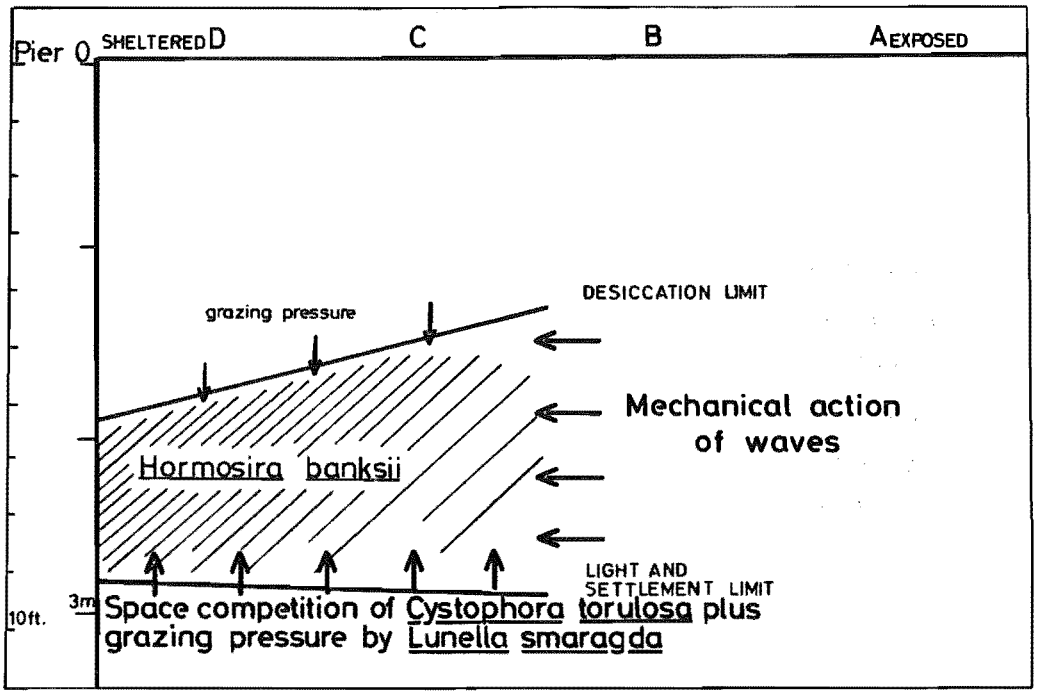

Pier 0
?? DESICCATION LIMIT ??
SHIFT WITH
SEASONAL
COVER OF
PORPHYRA
limit of heavy algal cover
Lunella smaragda
10ft.
3m
SHELTERED
D
C
B
A
EXPOSED

Figure 41.

This figure illustrates the vertical distribution of Cystophora torulosa in relation to the degree of wave action, as determined by transect studies, and the factors affecting the distribution, as determined by field observations and by experiments.

Figure 42.

This figure illustrates the vertical distribution of Lunella smaragda, within the littoral zone and the correlation of its upper limit with the upper limit of macroscopic algal growth.


Pier 0
SHELTERED D
C
B
A EXPOSED
DESICCATION LIMIT
grazing pressure
Mechanical action of waves
Hormosira banksii
LIGHT AND SETTLEMENT LIMIT
3m
10ft.
Space competition of Cystophora torulosa plus grazing pressure by Lunella smaragda

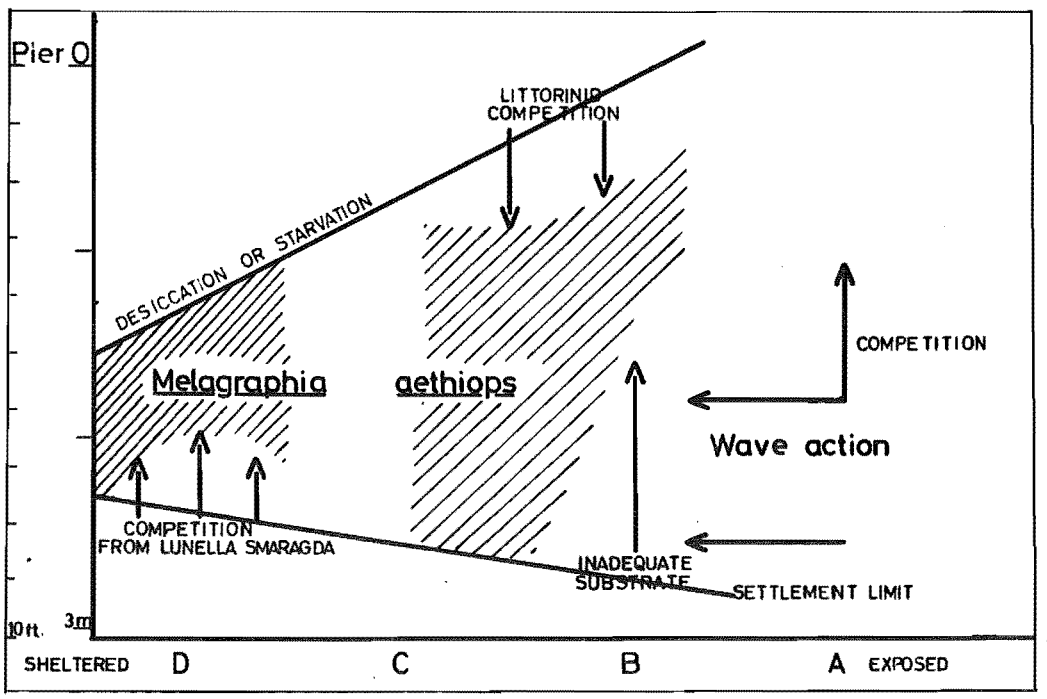
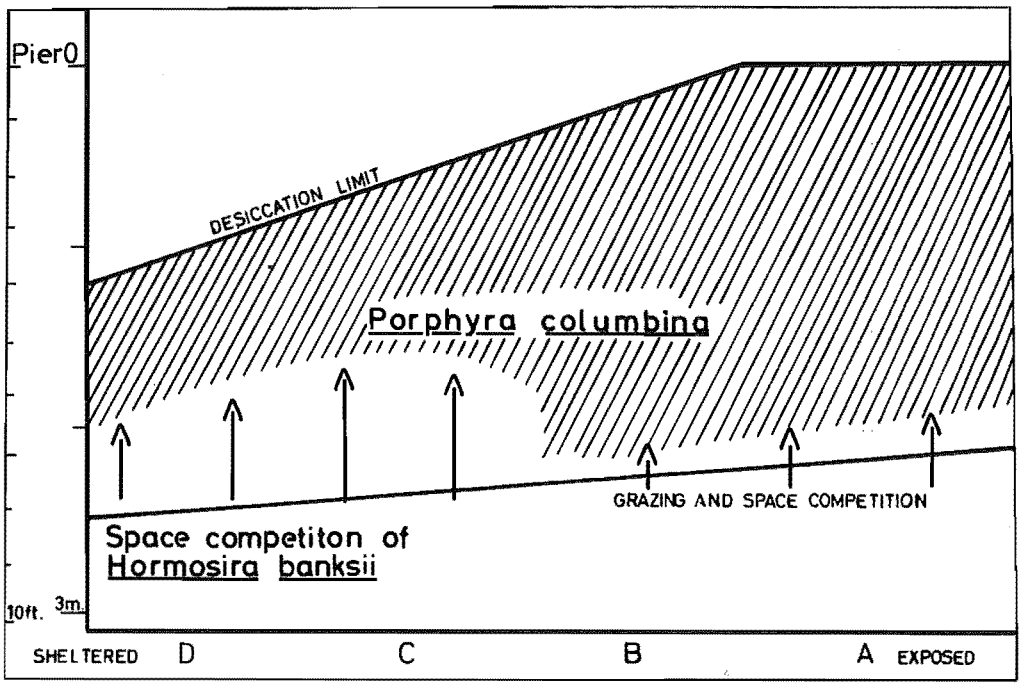

Pier 0
LITTORINID COMPETITION
DESICCATION OR STARVATION
COMPETITION
Melagraphia
aethiops
Wave action
COMPETITION FROM LUNELLA SMARAGDA
INADEQUATE SUBSTRATE
SETTLEMENT LIMIT
10ft.
3m
SHELTERED
D
C
B
A EXPOSED

Figure 43.

The distribution of Hormosira banksii showing the many factors that limit its distribution. It is noted that the upper and lower limits are only slightly affected by competition but that the concentration of the plants is lessened near the edge of the range by this competition. Diminished concentration is indicated by wider spacing of the shading lines.

Figure 44.

The distribution of Melagraphia aethiops and factors affecting that distribution. The central gap in the distribution represents transects that had extremely low or non-existent concentrations of M. aethiops due to inadequate substrate.


Pier0
DESICCATION LIMIT
Porphyra columbina
GRAZING AND SPACE COMPETITION
Space competiton of
Hormosira banksii
10ft. 3m.
SHELTERED
D
C
B
A EXPOSED

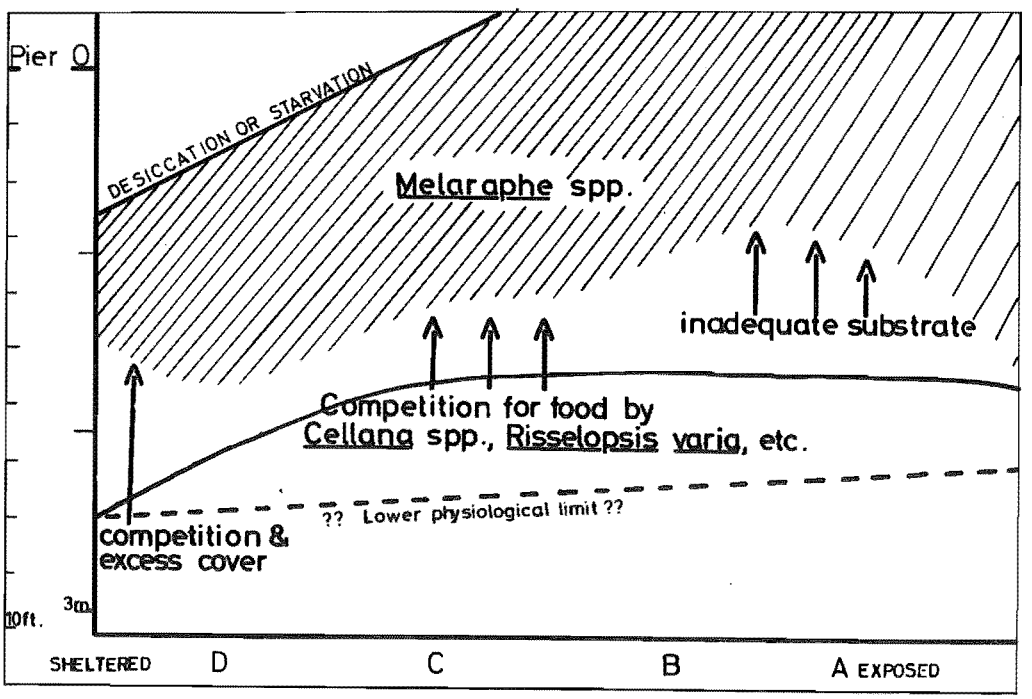

Pier 0
DESICCATION OR STARVATION
Melaraphe spp.
inadequate substrate
Competition for food by
Cellana spp., Risselopsis varia, etc.
?? Lower physiological limit ??
competition &
excess cover
10ft. 3m.
SHELTERED
D
C
B
A EXPOSED

Figure 45.

This figure illustrates the winter distribution of Porphya columbina. Particularly obvious is the effect of space competition by Hormosira banksii. The effect of grazing by molluscs was demonstrated in wave beaten areas but data for sheltered areas is still forthcoming.

Figure 46.

The distribution of Melaraphe spp. Such a sharp change of habitat occurs at the upper limit that it seems unnecessary to ascribe it to any one factor. However a desiccation effect would seem to be the major cause of this environmental change as well as the most limiting factor on the organisms themselves.

The lower solid line connects points at which solitary individuals have been found or to which the distribution has been shifted in field experiments. The doubtful submergence level is just that, doubtful.

Summary

1. The intertidal regions of the Kaikoura Peninsula were surveyed and the geography, geology, climate, and general hydrographic features are described.

2. The flora and fauna of the intertidal rocks were surveyed. A species list is given and the distribution patterns of the organisms are described.

3. A number of experiments were performed, in the laboratory and in the field, to determine the effects of various physical and biological stresses on the topographically dominant organisms. The results of the experiments are reported.

4. Field observations and experimental data were correlated and the effects of certain stresses were discussed. The major factors limiting vertical distributions were found to be: desiccation, light, and competition.

5. The distributions of Melaraphe spp., Melagraphia aethiops, Lunella smaragda, Porphyra columbina, Hormosira banksii, and Cystophora torulosa are discussed in detail.

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Appendix 1. (cf. I.B.).

The following maps represent observations of wave action on the shores of the Kaikoura Peninsula made during the period from 11 July, 1963, to 7 May, 1964. The method of observation and the description of the wave classes occurs in the body of this paper (cf. I.B. 3. c.). Each map represents an aggregate of observations made on two or more days.

The color code is as follows:-

Red	Class V
Orange	Class IV
Blue	Class III
Green	Class II
Yellow	Class I
White	Class O

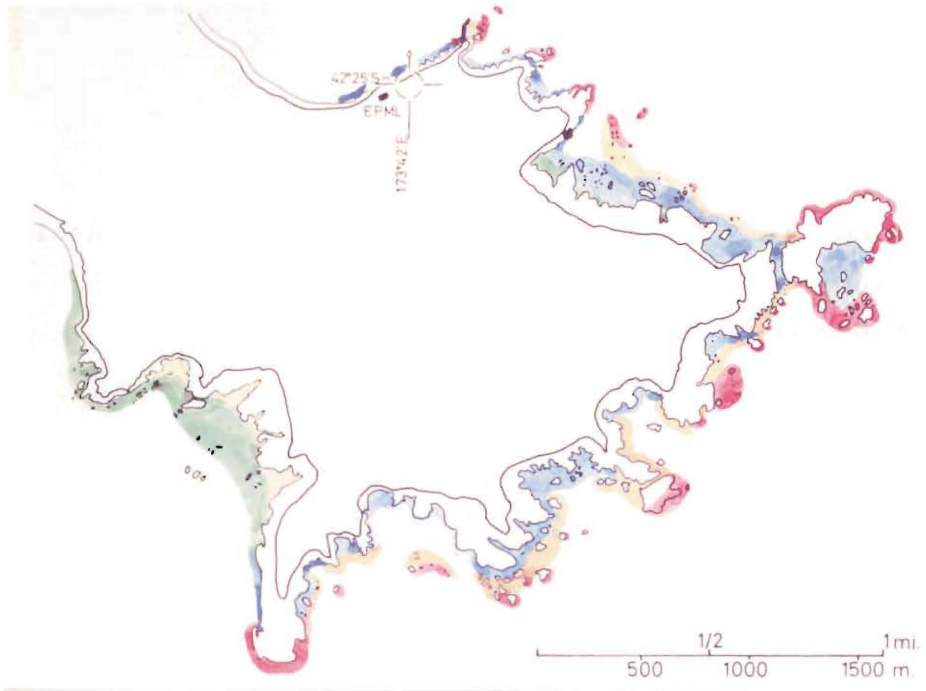
Wind velocity, wind direction, and tide levels are indicated on the overleaf of each map.

Figure 47.

A summary of wave action about the Kaikoura Peninsula at high tide, as observed during strong winds with a northerly bearing.

Figure 48.

A summary of wave action about the Kaikoura Peninsula at high tide, as observed during strong winds with a southerly bearing.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EPML
173°42'E
1/2
1 mi.
500
1000
1500 m.

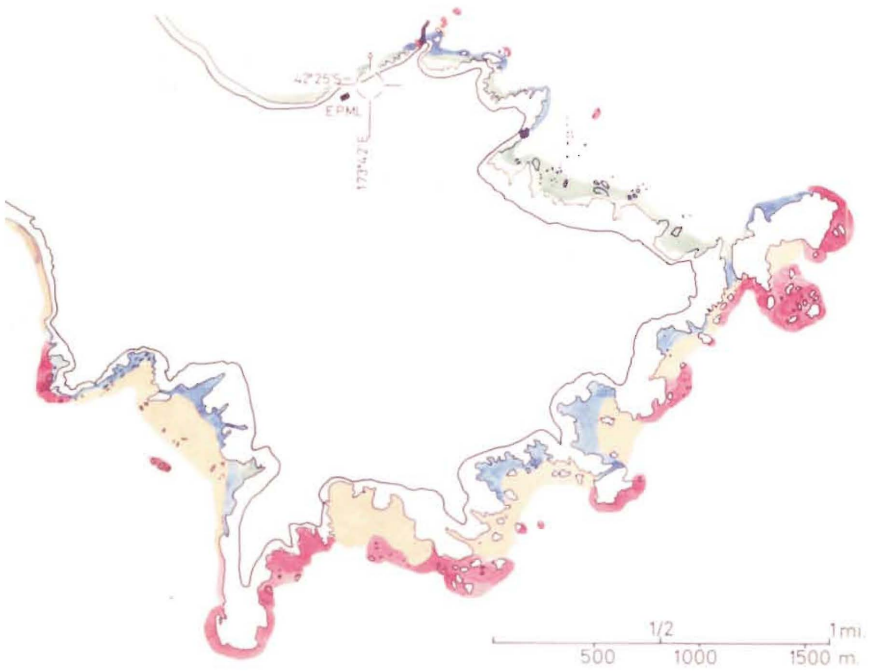
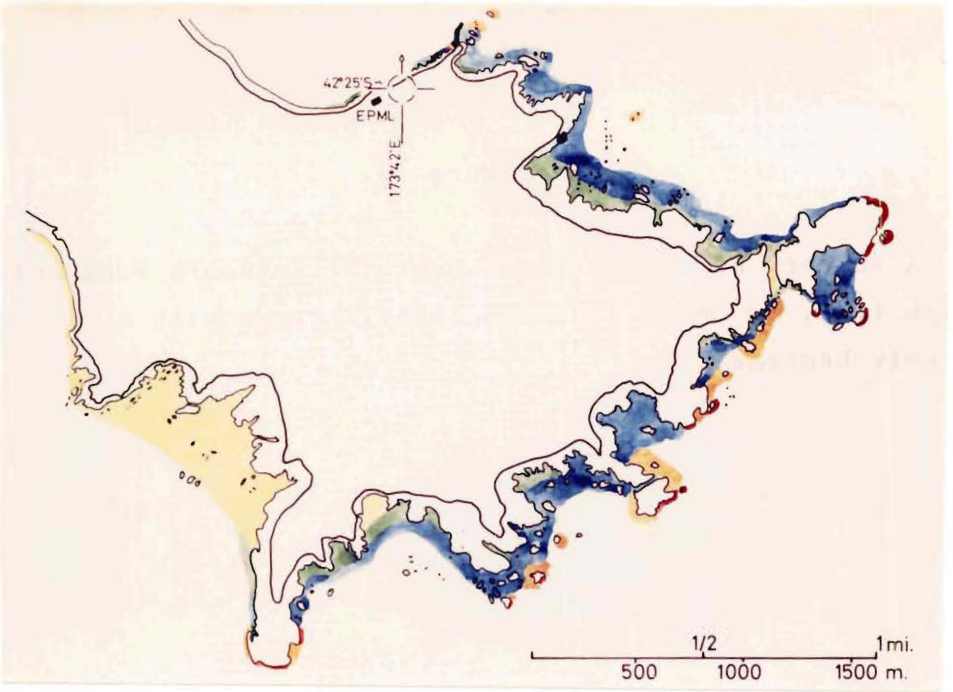

42°25'S
EPML
173°42'E
1/2
1 mi.
500
1000
1500 m.

Figure 49.

A summary of wave action about the Kaikoura Peninsula at high tide, as observed during gentle winds with a northerly bearing.

Figure 50.

A summary of wave action about the Kaikoura Peninsula at high tide, as observed during gentle winds with a southerly bearing.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EPML
173°42'E
1/2
1 mi.
500
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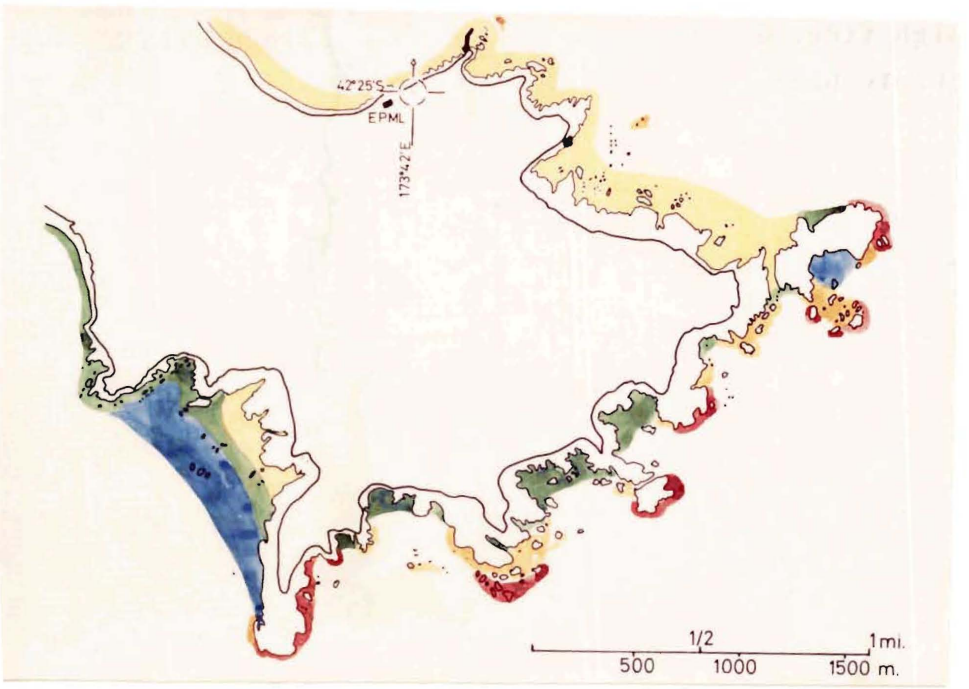
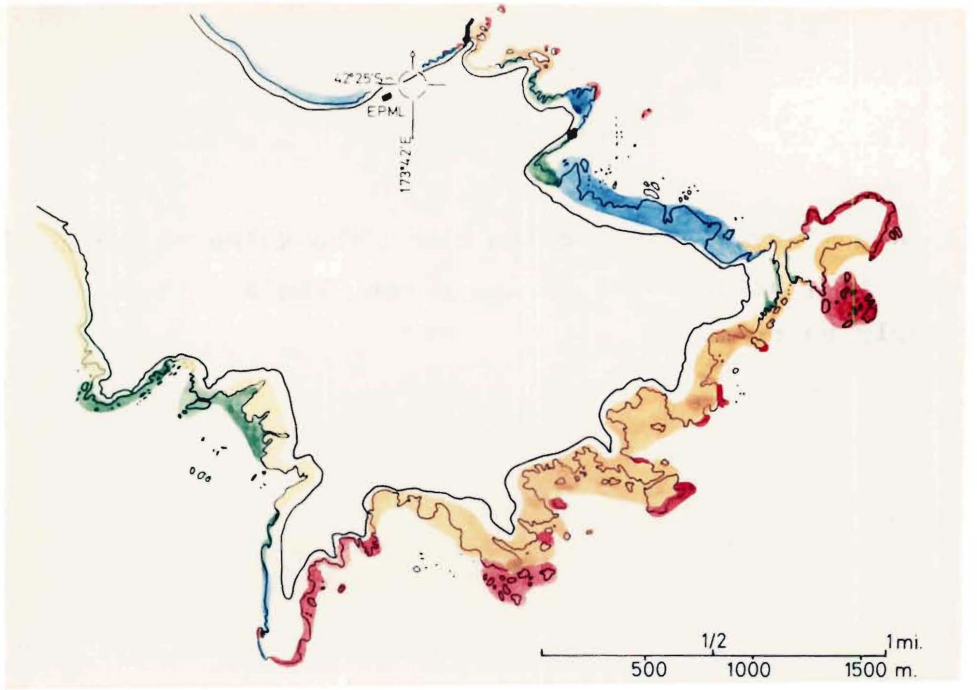

42°25'S
EPML
173°42'E
1/2
1 mi.
500
1000
1500 m.

Figure 51.

A summary of wave action about the Kaikoura Peninsula at mid tide, as observed during strong winds with a northerly bearing.

Figure 52.

A summary of wave action about the Kaikoura Peninsula at mid tide, as observed during strong winds with a southerly bearing.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EPML
173°4.2'E
1/2
1 mi.
500
1000
1500 m.

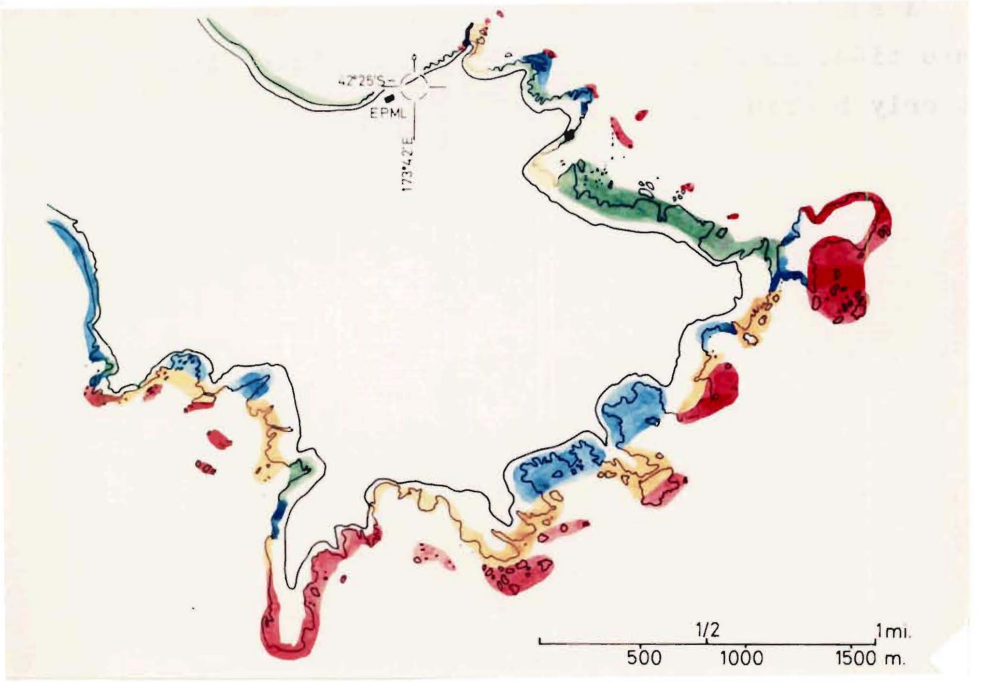
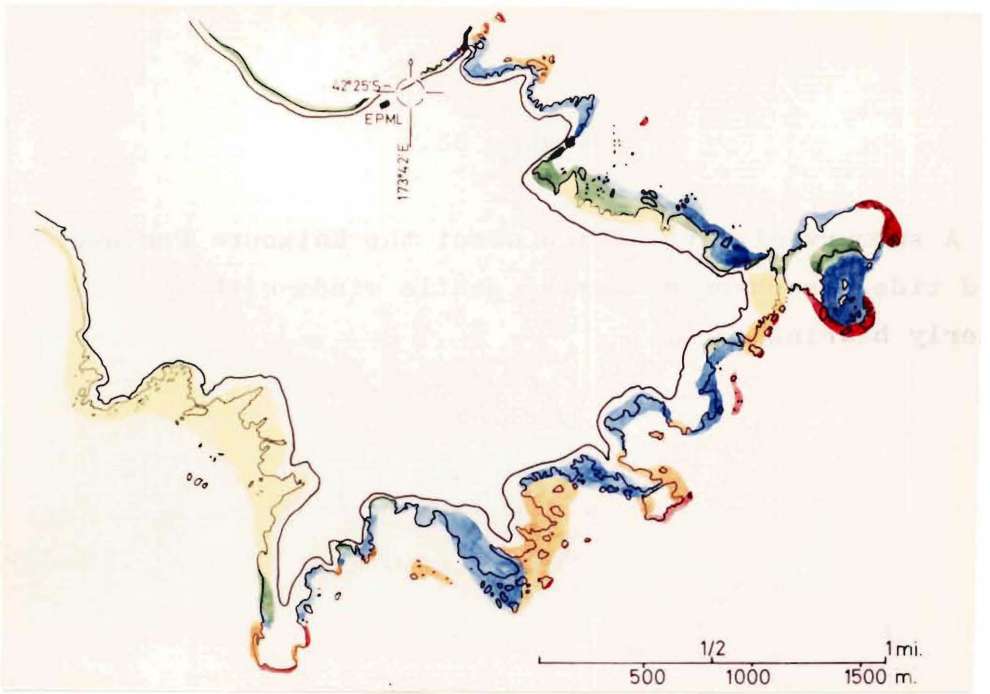

42°25'S
EPML
173°4.2'E
1/2
1 mi.
500
1000
1500 m.

Figure 53.

A summary of wave action about the Kaikoura Peninsula at mid tide, as observed during gentle winds with a northerly bearing.

Figure 54.

A summary of wave action about the Kaikoura Peninsula at mid tide, as observed during gentle winds with a southerly bearing.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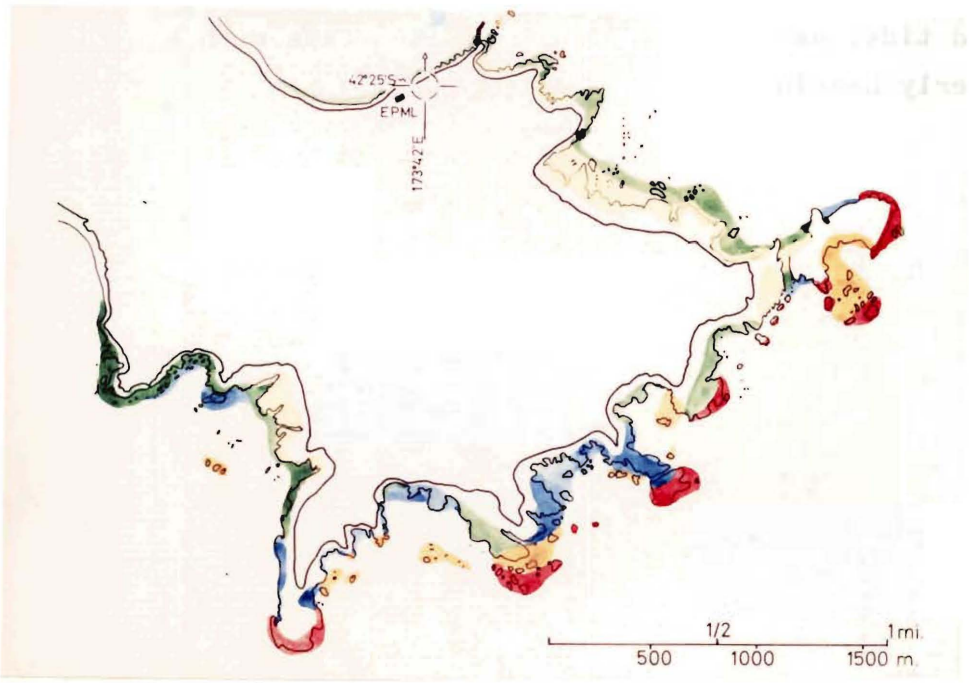
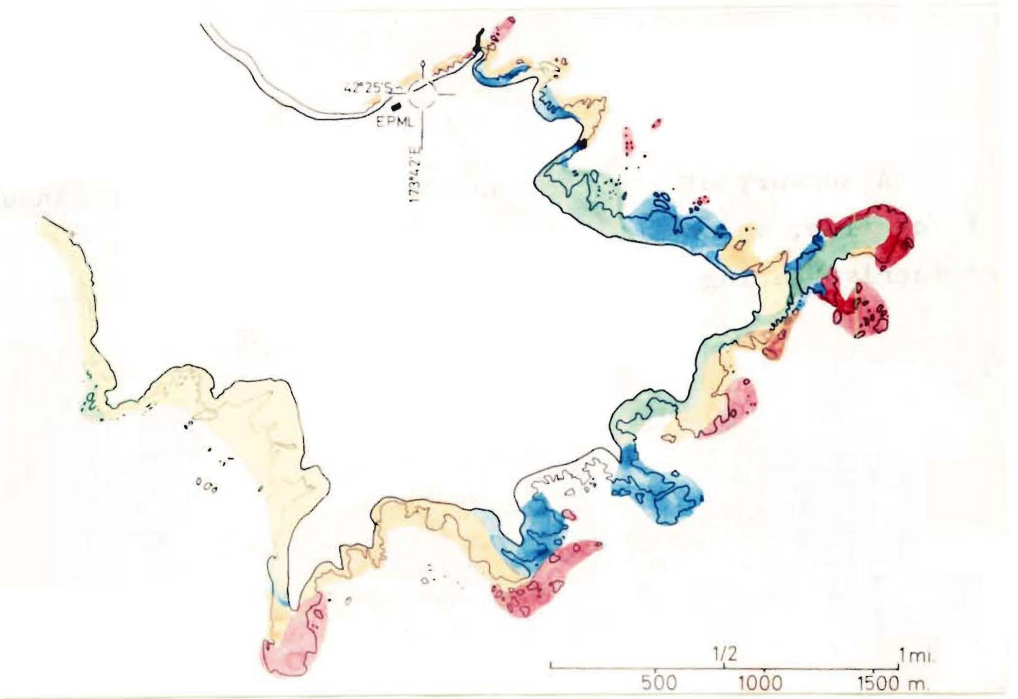

42°25'S
EPML
173°42'E
1/2
1 mi.
500
1000
1500 m.

Figure 55.

A summary of wave action about the Kaikoura Peninsula at low tide, as observed during strong winds with a northerly bearing.

Figure 56.

A summary of wave action about the Kaikoura Peninsula at low tide, as observed during strong winds with a southerly bearing.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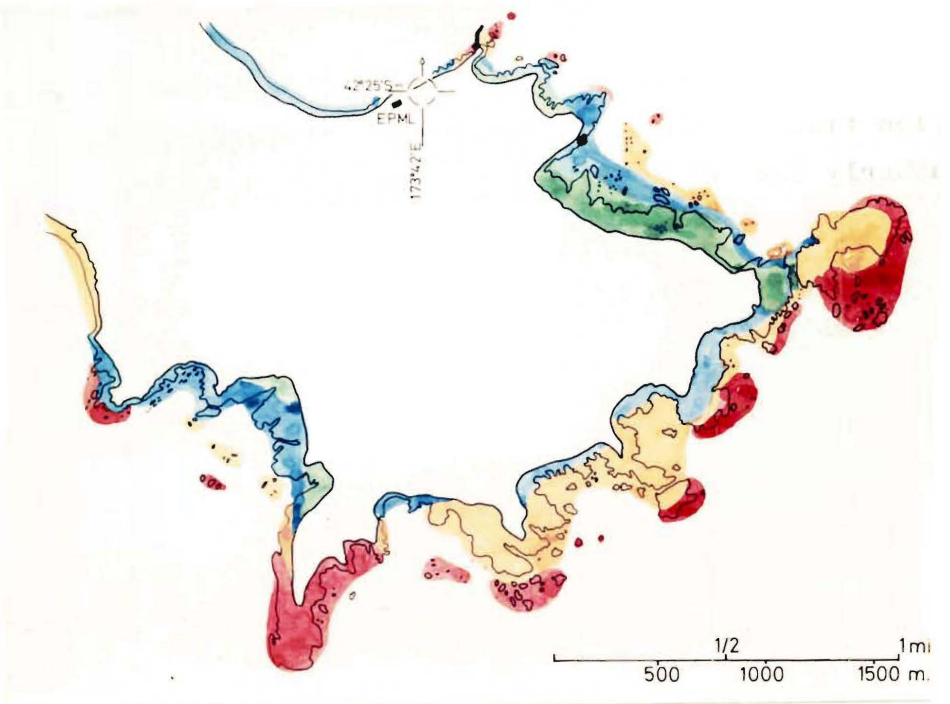
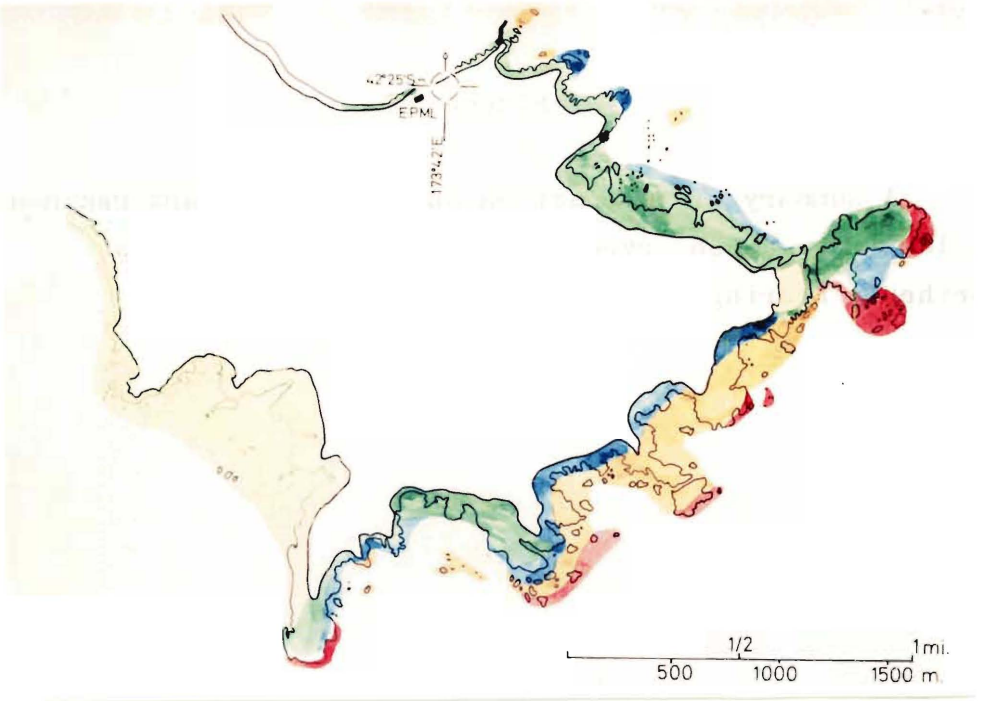

42°25'S
EPML
173°42'E
1/2
1 mi
500
1000
1500 m.

Figure 57.

A summary of wave action about the Kaikoura Peninsula at low tide, as observed during gentle winds with a northerly bearing.

Figure 58.

A summary of wave action about the Kaikoura Peninsula at low tide, as observed during gentle winds with a southerly bearing.


42°25'S
EPML
173°42'E
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1 mi.
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1500 m.

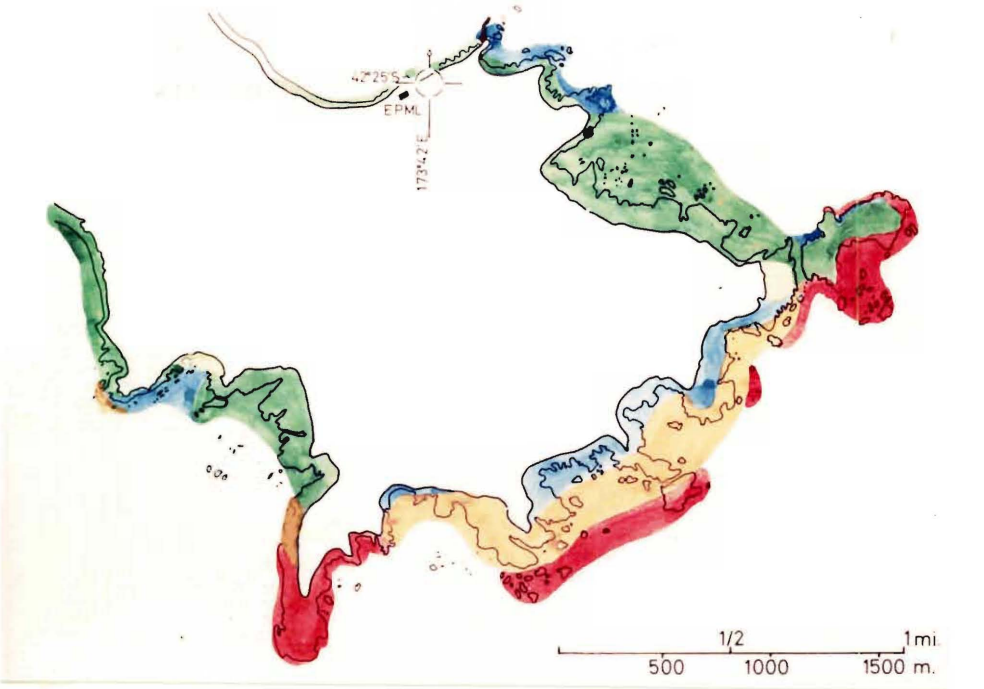
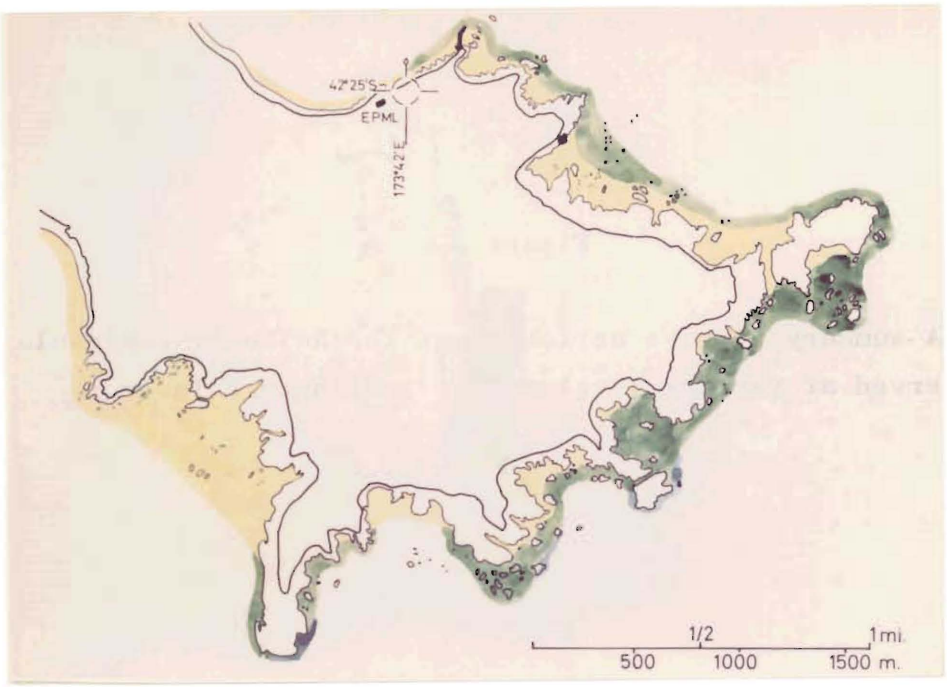

42°25'S
EPML
173°42'E
1/2
1 mi.
500
1000
1500 m.

Figure 59.

A summary of wave action about the Kaikoura Peninsula as observed at various levels after prolonged calms.


42°25'S
EPML
173°42'E
1/2
1mi.
500
1000
1500 m.

Desiccation Experiments (cf. II. B. 2. a.)

Equipment

Two heated chambers were used to perform the desiccation experiments described in this study.

The first desiccation chamber was constructed by placing two old laboratory tables side by side and building walls around the legs so that the chamber was formed under the tables. The table tops were of heavy wood and were considered adequate insulation. The walls were constructed of sheets of 3/8 inch cellulose fibreboard (trade name-Pinex) on three sides. On the fourth side, the wall was formed by placing two, discarded, glassed, cabinet doors on their sides so that there was a dead air space between the windows. All crevices and joins were covered with old newspapers. The floor space was also covered with fibreboard.

A 2000W electric heater was placed in one corner of the chamber. The heater was connected to a small simmerstat switch outside the cabinet. A max.-min. thermometer was hung near the center of the chamber.

With a bit of practice, and a certain amount of good luck, it was possible to establish a temperature in the chamber and to hold it constant to within four degrees Centigrade for twenty-four hours.

During experiments, it was necessary to open and close the chamber upon occasion to remove specimens. During these periods there was a marked drop in temperature. The temperature was re-established within fifteen minutes (usually much less) by manual control.

It will be recognized, by now, that the main virtue of this chamber was the low cost of its construction.

During one of the inevitable shifts occurring in a new laboratory it became necessary to construct a new chamber. This time, a large packing case was obtained from a local garage. The packing case had contained a new petrol pump. This case was lined with the fibreboard salvaged from the old chamber and part of one side was fitted with hinges and ball catches to form a door. Wooden shelves were fitted inside. A mercury thermometer was inserted through a cork in a small hole in the top of the case. A 1000W bar heater was placed in the bottom of the case and connected to the simmerstat switch on the outside. To all intents and purposes, we had constructed a rough version of the upright clothes drying cabinet, (to which use this chamber was also put).

This chamber proved to be a considerable improvement over the former model. The temperature control was constant to within two degrees Centigrade in twenty-four hours. Specimens were more accessible, and the heat loss upon opening the chamber was less, and more rapidly rectified.

Experiments

The inadequacies of the equipment precluded the possibility of establishing Thermal Death Points for the animals, such as Clark (1957) had done previously for Melagraphia aethiops, or constructing accurate comparative weight loss curves. Similarly, it was not possible to establish compensation points for the alga, as Trevarthen (1954) had done for Hormosira banksii. However, relative resistance to heat, or drying, could be established by subjecting several species to the same conditions at the same time. No absolute quantities were then necessary and the vagaries of the equipment were immaterial to the experiments.

Experiments were conducted on the animal series: Melaraphe cincta, M. oliveri, Melagraphia aethiops and Lunella smaragda. Experiments were conducted on two algal species: Hormosira banksii and Cystophora torulosa.

For all the experiments the temperature was maintained as close as possible to 35°C. This temperature was chosen because it represented a temperature slightly higher than reported air temperatures yet not so high as to be beyond the possibility of the local climate. This also allowed for the direct heating that can occur in the animal by direct exposure to sunlight. This temperature was also well below the Thermal Death Point reported for Melargraphia aethiops (Clark 1957).

When a hygrometer became available during the course of experiments, records were made of the relative humidity in the chamber. Field measurements were also made whenever it appeared that maximum drying should be occurring, i.e., summertime, mid-day, spring low-tides. The relative humidity in the cabinet was consistently 40% at the beginning of experiments. No reading lower than 58% was ever obtained over the rocks, even on the highest, driest rocks of the upper intertidal. The shingle road bed near the shores sometimes gave readings of 54%.

The hygrometer was a "hair" hygrometer guaranteed to ± 2% accuracy and tested by the supplier. Suspended on a wire rack it measured the air flow approx. 2cm. above the surface.

Animals were tested for survival by placing them in aquaria after drying. Ability to get up and move was taken as a survival criterion. Survival of 50% of the test group of any species was used as the comparative point.

Results

24 July 1964

Eleven trays were prepared, each containing 10 L. smaragda, 20 M. aethiops, and 30 mixed Melaraphe spp. The animals from one tray were placed in an aquarium jar. The remaining ten trays were placed in a large shallow tray containing fresh water. This was located in the desiccation chamber. A small quantity of sea water was added to one animal tray. At intervals, a tray was removed and the animals placed in an aquarium jar. The results are expressed in survival per-centages.

Desiccation time (hr.-min.)	Lunella	Melagraphia	Melaraphe
5:00'	100%	100%	100%
9:45'	"	"	"
20:00'	"	"	"
29:45'	"	"	"
44:00'	100%	75%	100%
57:45'	80%	75%	"
61:15'	30%	40%	"
63:15'	50%	0%	"
66:30'	60%	0%	"
Sea water specimens	100%	80%	100%
Aquarium control	100%	100%	100%

The order of survival indicated is Melaraphe spp. L. smaragda M. aethiops. That this was truly a desiccation effect rather than a thermal effect is suggested by the high survival rate of the specimens in the small quantity of sea water.

6 August 1964

Ten trays were prepared, each containing 10 L. smaragda, 20 M. aethiops, and 30 mixed Melaraphe spp. The animals had previously been conditioned for eight hours in the aquarium. Animals from one tray were returned to the aquarium, after being weighed. The others were weighed in groups, by species, and placed in the desiccation chamber. At intervals a tray was removed, the species groups weighed, and the animals returned to the aquarium to determine survival per-centages. Weight losses are reported as per-centages of original weight.

Desiccation time (hr.-min.)	Lunella survival	wt. loss	Melagraphia survival	wt. loss	Melaraphe survival	wt. loss
36:45'	100%		75%	3.6%	100%	0.6%
39:15'	100%	7.0%	0%	8.5%	100%	8.7%
41:00'	100%	6.2%	0%	9.8%	100%	20.1%
43:45'	100%	7.1%	35%	9.4%	100%	19.0%
60:45'	50%	9.0%	0%	11.3%	83%	13.4%
68:30'	100%	7.9%	0%	12.3%	100%	0.0%
84:00'	70%	8.8%	0%	12.3%	86%	15.1%
102:30'	0%	12.8%	0%	18.0%	86%	12.2%
116:30'	0%	13.1%	0%	16.8%	96%	17.7%
control	100%	0.2%	100%	1.2%	100%	-0.8%

The order of survival indicated is Melaraphe spp., L. smaragda, M. aethiops, as in the previous experiment. Irregularities evident in the rate of demise are evened out if the weight loss is used as a standard of comparison, rather than time. The difference in rate of weight loss is probably a result of uneven heating in the chamber.

7 October 1964

In previous experiments it was noted that there was an apparent relationship of size to desiccation resistance in M. aethiops. To check this, a collection of M. aethiops was sorted into size groups; small, medium, and large, roughly comparable to the second, third, and fourth year classes. Five trays were prepared. Each tray had five large, ten medium and ten small M. aethiops. These were then subjected to desiccation in the chamber. Results are expressed in survival per-centages.

Desiccation time (hr.-min)	Small	Medium	Large
36:00'	0%	90%	80%
40:15'	0%	70%	40%
49:30'	0%	20%	20%
59:15'	0%	20%	40%
66:45'	0%	0%	0%

The small M. aethiops were evidently more susceptible to desiccation than the larger specimens. This is in accord with the findings of Clark (1957) and with the field counts of this study.

30 October 1964

Because of the rapid demise of the smallest class of M. aethiops in the previous experiment, another attempt was made to ascertain an approximate survival rate for them. Five trays, each containing twenty M. aethiops of the second year-class, were prepared. These were placed in the desiccation chamber, one tray removed at a time, and the animals tested for survival. Results are expressed in survival per-centages.

Desiccation time (hr.-min.)	Survival
00:00' (control)	100%
5:10'	95%
19:00'	90%
23:00'	54%
30:00'	5%
41:00'	0%

20 January 1965

Ten specimens of C. torulosa of fairly uniform size, and twenty specimens of H. banksii of two size groups, small and medium, were placed in the desiccation cabinet after being blotted and weighed. One specimen of C. torulosa and one from each size group of H. banksii were removed at intervals, weighed and the viability of the apical cells tested with 2-3-5 triphenyl tetrazolium chloride, a vital stain commonly used in germination tests of seeds of crop plants.

The stain technique failed to produce results. Only the per-cent wt. loss was obtained from this experiment.

Desiccation time (hr.-min.)	Wt. loss C. torulosa	H. banksii small	medium
0:00'	0%	0%	0%
0:35'	5%	7%	9%
1:15'	105%	19.5%	14%
1:45'	29%	35%	24.5%
2:15'	29%	42%	30%
2:30'	33%	44%	31%
2:45'	32%	53%	50%
3:00'	41%	53%	34%
6:45'	60%	71%	61%
8:05'	72%	64%	55%

The specimens removed at 6:45' and 8:05' were dry, dark, and brittle. All previous specimens were flexible, slightly darkened in patches, and covered with mucous.

18 February 1965

The failure of the previous experiment to produce any evidence concerning the relative survival of H. banksii and C. torulosa when subjected to desiccation conditions led to another attempt in which the time intervals for removal were shortened and the specimens removed to a large out-of-doors aquarium tank for recovery.

Twelve specimens of C. torulosa and twelve of each of two size groups of H. banksii were placed in the desiccation chamber. One specimen of C. torulosa, and one from each group of H. banksii were removed at intervals, examined for superficial changes, and placed in the aquarium where they were observed for several weeks.

Desiccation time (hr.-min.)

0:30' C. torulosa showed some minor spotting.
H. banksii dimpled but not discolored.

1:05'

1:30' C. torulosa showing discoloration of apical bundle of branchlets.

2:00' H. banksii showing first signs of discoloration.

2:40'

3:10'

3:50' H. banksii terminal segments discolored.

4:20'

4:55'

5:20' C. torulosa better than 50% discolored.
H. banksii better than 50% discolored.

5:50' " "

6:20' " "

Examination of specimens two weeks later indicated that all had survived the desiccation but that discolored areas were indeed severely damaged. Colored patches had not returned to shape, or color, and often showed signs of decay. It had been expected, in line with the previous experiment, that the last plants removed from the chamber would be totally desiccated. Unfortunately, this did not prove to be the case. However, the earlier appearance of discoloration, and particularly the earlier discoloration of the apical areas, of C. torulosa indicates that this plant is more susceptible to desiccation than H. banksii. Field observations show the same characteristic discolorations, on both species, to be much more prevalent in the upper part of the species' vertical range.

Salinity Dilution Experiments (cf. II. B. 2. c.)

Equipment

The equipment for this experiment consisted of nine battery jars of approximately two liter capacity which served as aquaria. Two plastic "jerry-cans" which served as reservoirs to receive overflow. Two metal containers, lined with an epoxy-resin compound and fitted with taps, to serve as "header" reservoirs. The header reservoirs were placed on the top of the back shelf of a laboratory bench. The aquaria were placed upon the working surface of the bench. The jerry-can reservoirs were placed under the bench. Water flow from the header reservoirs was directed to the aquaria through polyethylene tubing. Automatic siphons of glass tubing provided control of the overflow which was directed through more polyethylene tubing to the jerry-can reservoirs. When the header reservoirs were exhausted the overflow reservoirs were emptied back into the headers. Thus two parallel recirculating systems were formed.

Experiment

It was thought to be desirable to determine the relative tolerance to diluted sea-water of the three animal groups under investigation. It is to be supposed that animals higher on the shore would be subjected to such dilution from seepage and rainfall in greater degree and more often than the animals further down the shore. Animals were collected, along with rocks from their native habitat, and placed in the aquaria. Some were put into one re-circulating system which contained 100% sea-water. These were controls. Those placed into the other re-circulating system were subjected to dilute sea water.

When more than 50% of the population under dilution stresses showed signs of distress, they were removed to the 100% sea-water to determine their recovery ability. A fifty per-cent mortality time was used as a comparative point.

Results

5 July 1964

One control and two experimental aquaria were loaded with twelve L. smaragda, each. One control and two experimental aquaria were loaded with fourteen M. aethiops each. One control and two experimental aquaria were loaded with sixty mixed Melaraphe spp., each.

The controls were subjected to re-circulated 100% sea-water. The experimental animals were subjected to an approximately 75% dilution of the same sea-water. (Salinity determinations: sea-water 34.3 p.p.t. expressed as chlorinity. Diluted sea-water 26.7 p.p.t.).

Distress symptoms were first noticed in M. aethiops after two days. In four days, 75% of the M. aethiops were distressed. These were tested for survival.

After five days, the L. smaragda specimens all began to show signs of distress and were removed to test survival. At this time, all of the M. aethiops were removed from the experiment as the mortality exceeded 50%.

On the sixth day, L. smaragda mortality reached 50%.

On the seventh day L. smaragda were removed from the experiment.

As the Melaraphe spp. showed no signs of distress by the eighth day, the salinity was further reduced to approximately 62.5% sea-water. (Salinity determination of 21.5 p.p.t.).

On the ninth day the salinity was further reduced to approximately fifty percent. (Salinity determination 17.1 p.p.t.).

On the eleventh day, nearly all the Melarphe spp. showed signs of distress and the experiment was terminated.

Order of survival indicated is Melaraphe spp., L. smaragda, M. aethiops. The degree of difference between Melaraphe spp. and the other species was considerably greater than the difference between L. smaragda and M. aethiops.

Submergence Experiments (cf. II. B. 1.)

Equipment

Battery jar aquaria, fibreglass gauze of the type used for screening windows, nylon cord, nylon zipper fasteners, 3/16" soft steel concrete reinforcing mesh (1/2" squares), lug bolts, soft steel straps, assorted nails and carriage bolts and scrap lumber.

For field experiments, a frame ten feet long by one foot square was constructed by bending a ten-by-four sheet of reinforcing mesh lengthwise three times and welding the free edges. This frame was then partitioned into one foot sections by welding more reinforcing rods into place through the cage. Small cages were then constructed to fit into each of these sections. These cages consisted of a wooden floor and ceiling with a single strip of fibreglass gauze forming the sides. The ends of the fibreglass gauze strip were joined with a nylon zipper fastener to form a door. The cages were inserted into the sections of the steel frame and the floor of each was bolted through to the ceiling of the cage below. This formed a single unit of ten separate cages. The steel frame was fastened to the pier by two large clips made of soft steel strap which were bent to fit a cross brace between pilings. On each clip was a hasp. A steel strap was fitted through the hasps and the back of the steel frame. Further, the top of the frame was fastened to the decking of the pier by a rope. This placed the ten cages vertically in such a way that three were below the lowest water line and the others extended through intermediate degrees of submergence.

For laboratory experiments, the battery jar aquaria were

fitted with tops of fibreglass gauze tied in place with the nylon cord.

Experiments

The experiments were designed to test the hypothesis that the animals and plants under observation were not limited vertically by simple submergence factors. This could be tested by isolating individuals in a totally submerged condition for a long period. The animals were to be given a natural substrate, with food organisms, but separated from possible competitors.

Field observations indicated that only Melaraphe spp. M. aethiops, and P. columbina required this testing.

Results

8 September 1964

The field cage was placed in such a fashion that three cages would be totally submerged during the two months to follow. The suckback of wave action was allowed for. Six M. aethiops were placed in one cage at a level equivalent to their normal lower limit, six in a cage that would be totally submerged, and six in a cage that would be intermediate between their normal lower limit and total submergence. Twelve mixed Melaraphe spp. were placed in a cage at a level equivalent to their normal lower limit, twelve in a totally submerged cage, and twelve in a cage of intermediate level. Pieces of rock from the area in which the specimens were collected were placed in each cage.

On the 10th of September, a storm tore the cage from the pier and deposited it on the bottom. The cage was recovered by skin diving two weeks later. A number of the cages were torn and the animals missing.

However, all of the animals recovered were still alive. This was encouraging, though not conclusive.

15 November 1964

The repaired cage was placed in position again with the same numbers of animals, at the same levels, as in the previous experiment. It lasted one week to ten days. The exact date upon which it broke loose could not be determined. Upon recovery, sixteen days after initiation of the experiment, all of the animals that had not escaped were alive. Though the construction fault responsible for the failure was discovered, the method was abandoned.

9 January 1965

Eight battery jars were fitted with fibreglass gauze covers. Four contained each five M. aethiops and rocks from the area of collection. Four contained each five Melaraphe cincta and ten M. oliveri with rocks from the area of collection. These were placed in a concrete aquarium tank, through which fresh sea-water was in constant circulation, in such a way that three from each set were totally submerged with the tops uppermost and the fourth, a control, was set on its side only partially submerged.

During the third week of the experiment, when all laboratory personnel were absent, the circulating sea-water system broke down. A strong sulfide deposit formed in all the aquaria. Circulation was restored on the fourth of February and within a week the sulfide had been cleared. The experiment was terminated on the 17th of February, five and one-half weeks after initiation.

Results are reported in per-centage survival.

	Melagraphia aethiops	Melaraphe cincta	M. oliveri
Control	100%	80%	100%
1	80%	0%	0%
2	100%	0%	20%
3	100%	20%	0%

While it appeared that M. aethiops could survive both submergence and sulfide, it was thought that the few survivors of the Melaraphe spp. indicated that the experiment could be profitably re-run.

17 February 1965

The previous experiment indicated that M. aethiops could survive considerable submergence but left some doubt as to the ability of Melaraphe spp. Accordingly, three tanks of M. aethiops, the control and two experiments, were left in the aquarium. Four fresh aquaria were outfitted, each with twenty Melarphe oliveri and ten M. cincta. Three jars were totally submerged and one partially submerged as before.

A manifold box was fitted to the incoming sea-water hose, so that each jar had a separate supply of sea-water to prevent sulfide accumulation. This entailed some manipulation of the jars while submerged. Small rents were made, unobserved, in the gauze covers and many Melaraphe spp. escaped during the course of the experiment - including a few that crawled up the inlet hoses.

The experiment was terminated on 19 March 1965. At this time, the M. aethiops had been submerged for seventy-three days and the Melaraphe spp. for thirty-one days. The results

reported indicate the survival per-centages of those animals remaining in the cages.

	Melagraphia aethiops	*Melaraphe cincta*	*M. oliveri*
Control	100%	100%	100%
Experimental	90%	86%	100%

Despite the fact that lack of time prevented a determination of the total time that these three species can withstand total submergence, it was felt that the evidence indicated that submergence did not account, in any physiological way, for the lower limits of distribution in the field.

Interspecific reaction field strips (cf. II. c.)

Equipment

A garden how, putty knife, masonry chisel, hammer, and assorted wire brushes.

Experiments

The belief that shore organisms occupy a vertical range that is often less than that caused by physiological limitations is widespread. Commonly, the modification of the vertical limits is attributed to interspecific competition factors. That the lower limits of some animal species, i.e., Melaraphe spp. M. aethiops, was not entirely physiological was indicated by the results of submergence experiments (cf. V. 2. c.). The exact coincidence of vertical limits of certain plant species, i.e., P. columbina-H. banksii, H. banksii-C. torulosa (slightly overlapping), indicated that this could be a factor in their distribution. While it was recognized that the reactions involved might be very complex, it was decided to test them in the field as though they were simple two-species interactions. This was done by removing, or reducing, the population of one member of the suspected interacting pair and measuring the reaction of the other member. Similar experiments had been performed by other workers, in other places. Castenholz (1961) excluded littorinids from small areas of intertidal rocks by means of wire cages and described a relationship between littorinid population and diatom growth. He also indicated a similar relationship between limpets and diatom growth. Southward (Southward, in Crisp 1964) cites several studies that have demonstrated the effect of limpet grazing upon algal distribution.

Connell (1961a) has shown that interspecific reactions can cause the separation of two species of barnacles whose physiological ranges would overlap. Finally, Luckens (1964) has shown that several species of New Zealand algae and animals may settle and develop beyond their normal shore range.

General notes were kept, in diary form, of the changes occurring on each strip. Quite often the changes were significant, and did not involve the species that were being tested.

Results

3 September 1963

The first experiment was established upon a rock face near the end of Avoca Point. The experimental surface faced eastward on a long, deep, and narrow surge channel. The experiment extended from the top of the rock mass which was 0.7 ft. (21 cm. approx.) above the barncle line, (and below high water) into the sublittoral.

A median strip, one meter in width, was cleared of limpets and macroscopic algae. Two border strips, each 0.5 m. were cleared of nearly all plants and animals. The strip was maintained by fortnightly removal of limpets for seventeen and one-half months.

Lateral migration of limpets on to the strip was initially checked by marking 137 limpets of the areas bordering the strip. None of these were found on the strip during the first two weeks. Fortnightly records indicate that most of the immigrants were small limpets coming from the sublittoral part of the strip or from the lower areas lateral to the strip.

This view did not take into account the known "homing" behaviour of these limpets as was later shown by a night visit to the strip. After clearing the limpets on the afternoon of 19 January 1965, the strip was visited on the following low tide, at night. Twenty-five large limpets, obviously lateral migrants were found upon the strip! That they were lateral migrants was indicated by their position and by the large number that were encrusted with barnacles. That the limpet grazing pressure had only been reduced, not nearly eliminated, makes the striking changes more significant than if this pressure had been totally eliminated. These changes have been summarized and discussed in the body of this paper (cf. II. C. a.) and will not be repeated here.

11 May 1964

On Wairepo Flats a strip one meter wide and seven meters long was cleared of H. banksii. The strip extended from the upper limit of the H. banksii seaward. Nothing else was removed from the strip. The strip terminated at a channel that held water at all times. (Pl. 19).

15 May 1964

On Wairepo Flats, another strip was cleared near the seaward edge of the platform. The strip was one meter wide and five meters long. It extended from a high point that was clear of H. banksii, and that had a growth of P. columbina the previous season, to the C. torulosa band. This strip was cleared of all macroscopic growth, except for some patches of prostrate Corallina officinalis. (Pl. 20).

Both strips were expected to demonstrate the validity

of the hypothesis that P. columbina did not grow at these levels because of the space competition of H. banksii. No P. columbina was observed on either strip during the following winter, although it was present a short distance above each strip.

As other evidence indicated that this was a valid hypothesis, it was assumed, at first, that the strips had been established too late in the season. Further observations indicated that P. columbina continued to settle until mid-June, however.

Other reactions were noted. Scytosiphon lomentaria appeared on the strips. S. lomentaria has a vertical range similar to P. columbina and a similar season, often occurring in mixed stands with P. columbina. Great quantities of Colpomenia sinuosa and Leathesia difformis appeared on the rejuvenated C. officinalis during their normal seasons. Large numbers of L. smaragda and M. aethiops were constantly present on the strips.

1964 was not a good year for P. columbina, in contrast with 1963. Experience with the effect of limpet grazing on more exposed situations, notably on the Avoca Point experiments, led to the hypothesis that the large numbers of L. smaragda and M. aethiops prevented the development of any P. columbina that may have settled on these strips.

To test this hypothesis another experiment was devised the following season (15 March 1965). The metal framework from the submergence experiments was modified by cutting off one side. Many holes were drilled into the rock on the experimental strip near the platform edge. The cut edges of the framework were placed into these holes.

A fibreglass strip was then laced around the framework. The holes and the floor of the enclosure were then concreted so that a fence was formed around a strip ten feet long by one foot wide (Pl.21). This strip is currently under observation.

11 May 1964

C. torulosa was stripped from an area one meter wide by six meters in length. This strip extended through the overlap of range of H. banksii and C. torulosa on Wairepo Flats. This strip was intended to demonstrate the hypothesis that C. torulosa was a space competitor with H. banksii. (Pl. 22).

It was observed that C. torulosa settled constantly through the year and, in the lower parts of the strip, grew much faster than H. banksii. The fresh growths of C. torulosa were removed regularly. H. banksii exhibited a marked increase of settlement and growth during the Spring and Autumn. It became evident that H. banksii would settle and grow to the bottom of the range overlap, and a very little bit below. Over the course of a year it also became evident that the H. banksii at the bottom of the strip grew more slowly than that at the top. Conversely, C. torulosa grew more rapidly at the bottom. The concentration of H. banksii was increased a great deal on the strip indicating that space competition was a factor in determining the final concentration of H. banksii in its lower range. It was also felt that support was given to the hypothesis that the lower limit of H. banksii is either a true physiological limit, or only slightly modified. This is in accord with the research of Trevarthen (1954) who attributes the lower limit of H. banksii to lack of sufficient light.

Secondarily, a substrate preference was noted. C. torulosa established best in heavily silted patches of Corallina turf. H. banksii established best in lightly silted Corallina turf, or in small declevities in the prostrate form of Corallina.

Plate 19.

A competition test-strip on Wairepo Flats. This was part of an attempt to extend the lower distribution of Porphyra columbina into the Hormosira banksii band. Only H. banksii has been removed from this strip. The strip is approximately one meter wide. (Photograph R.A. Rasmussen, 11 June 1964).

Plate 20.

A competition test-strip on Wairepo Flats. Another attempt to lower the distribution of Porphyra columbina. This strip was scraped with a garden hoe to remove all the macroscopic plant and animal life. Some of the Corallina officinalis remained. The strip is approximately one meter wide. (Photograph R.A. Rasmussen, 11 June 1964).

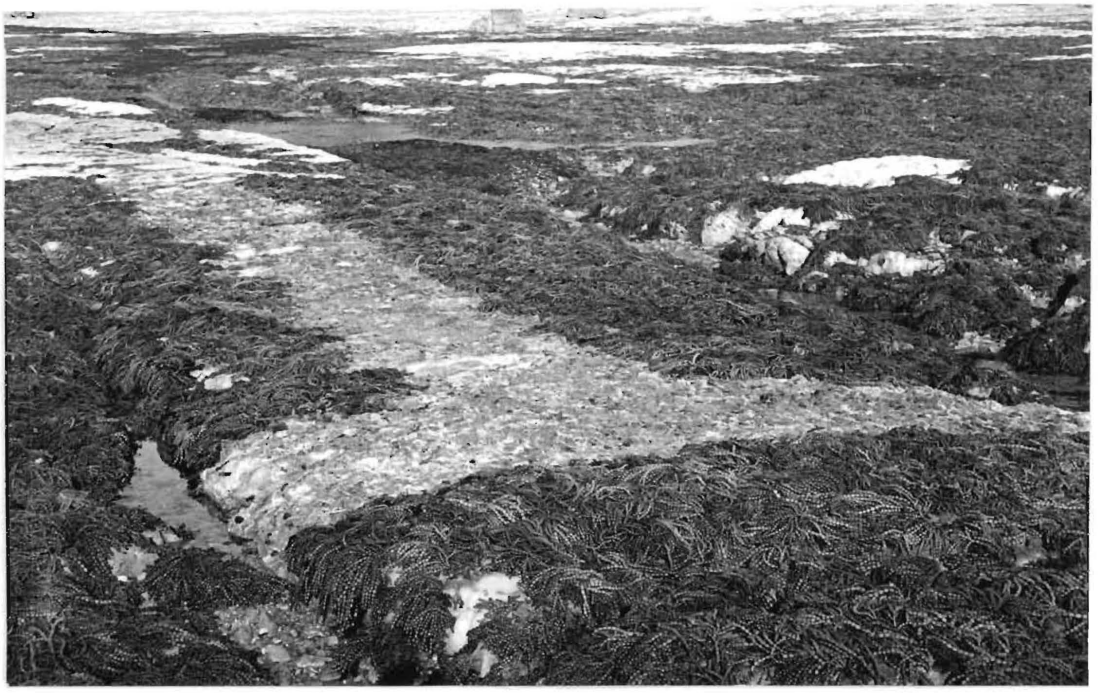


Plate 21.

The animal exclusion barrier erected the following Summer on the strip shown on Pl. 20, after a failure of Porphyra columbina to establish on the test-strip. The fibreglass gauze fence is six inches high. The cage is ten feet long and one foot wide. (Photograph R.A. Rasmussen, 7 April 1965).

Plate 22.

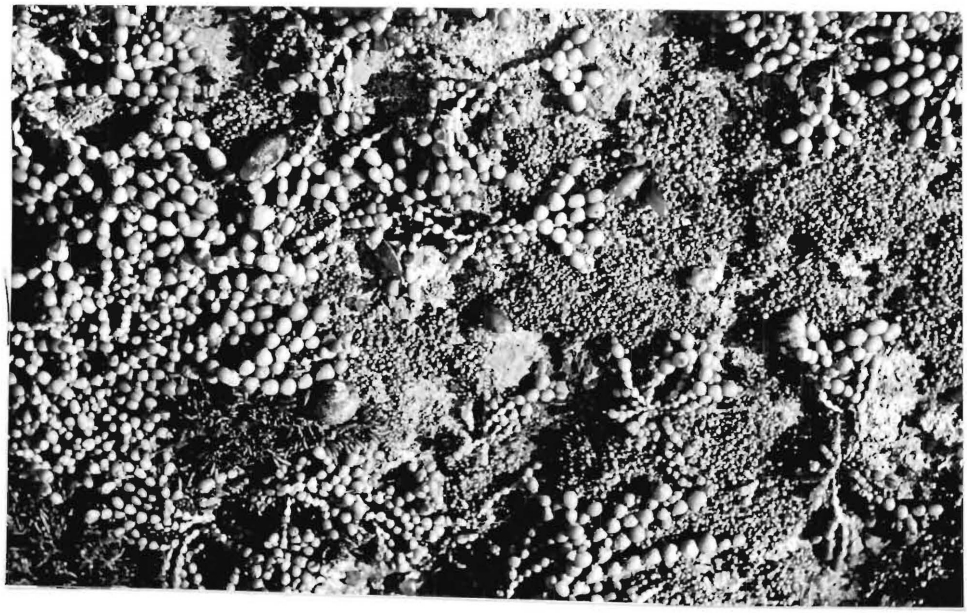
A competition test-strip on Wairepo Flats from which the Cystophora torulosa was removed to enable Hormosira banksii to establish below its normal range. The strip is just over a meter wide. (Photograph R.A. Rasmussen, 9 June 1964).

Plate 23.

Hormosira banksii settlement nine months after the establishment of the test-strip depicted on Pl. 22. An ample demonstration that H. banksii will settle and establish in heavy concentration at this level. (Photograph R.A. Rasmussen, 18 March 1965).

Plate 24.

Chamaesipho columna settlement on the barrier strips of the Avoca Point experimental strip. All animals and plants had been cleared from this area and the gastropod grazers were removed fortnightly. Clearly shown is the tendency to settle in surface irregularities. The scale is eight inches. (Photograph R.A. Rasmussen, 18 February 1965).



Porphyra columbina: comments on annual yield and commercial possibilities.

The use of various species of the genus Porphyra for human consumption is of great importance in certain heavily populated areas. The outstanding example would easily be Japan, although it is also a market commodity in Ceylon and parts of China. It is known that the New Zealand Maori also included the local species, P. columbina, in his long list of foods from the shores.

P. columbina is not currently harvested on a commercial basis in New Zealand. Because of known rising prices for the "amanunori", P. tenera, in Japan, and the evidently large standing crop on New Zealand shores, it was decided that a preliminary survey would be made of the harvestable P. columbina on the Kaikoura shores.

P. columbina has two stages in its life-cycle. During the winter months it covers the rocks from "effective" ELWN to EHWN (Fig. 21). In the summer this form disappears almost entirely. The alternate generation is not known, but it is inferred from other species of the genus that it is likely to be a fine filament that bores into shells or soft rock. The alternate stage of P. umbilicalis (L.) Kutz var. laciniata (Lightf) J. Ag. was discovered to be a filament previously known as Conchocoelis rosea Batters by Drew (1949, 1954). The "Conchocoelis" stages of several other species have since been described. In 1952, Drew and Richards (1952) by inducing infestation in the laboratory, demonstrated that the "Conchocoelis" stage of P. umbilicalis var. laciniata inhabited the plates of the barnacle Pollicipes cornucopia.

Two species of Pollicipes are found on the Kaikoura shores, P. spinosus, which is common, P. sertus which is less common (identification has been challenged and is being checked), and a related barnacle Calantica villosa. It only remains for someone to investigate this interesting problem.

A survey of the peninsula shores was made during the second week of June in 1964. First, shore rocks were scanned with binoculars from the cliffs. The location of all sizeable patches of P. columbina were marked on a map of the peninsula. During the following days, each of these localities was visited, the extent of the patch recorded on a grid map, and the per-centage covered by P. columbina estimated. Only "pure" stands of P. columbina were considered. Many patches were "mixed" stands containing a high per-centage of Scytosiphon lomentaria. In determining the final area of standing crop, only areas easily accessible on foot were considered. It is believed that by applying these stringent qualifications fully 50% of the P. columbina on the peninsula was eliminated from the survey. The results show that the major concentrations of harvestable P. columbina are on Lighthouse Point, Seal Reef, Mudstone Bay Flats, and Sharkstooth Point. A total of 29,950 square meters of P. columbina crop were determined to be harvestable from these areas.

To determine the yield from these patches, a square meter area was harvested (with clippers), dried, and weighed from each of the following locations:

(1) Lighthouse Point on the high points near the south end of Wooloomooloo Channel. 180g.

(2) Lighthouse Point on low, well drained rocks. 356g.
(3) Two square meters from the experimental strip at Avoca Point (cf. II. C. 1. a). 657g.
(4) Lighthouse Point, near (1). 146g.

These figures indicate an average of 267 g./m.^{2} or a total first-cutting harvest of approximately 7,787 Kilograms (dry weight) or, just over 8.5 tons. After about six weeks, it was noted that there was a considerable regrowth on cut squares. Square (1) was re-harvested and yielded 91.7g. This indicates the possibility of taking two cuttings, though the second was only 50% of the first.

Comparisons of photographs taken in 1963 with photographs and observations in 1964 show that 1964, the year of the survey, was not a highly productive year for P. columbina. This is further indicated by experience with the experimental strip on Avoca Point.

It has been observed that P. columbina grows best on frequently wetted but well drained surfaces. Estimates from the survey indicate that approximately twice as much area is covered with non-harvestable P. columbina as is covered with harvestable. Much of this unsuitable material was either too short or was mixed with quantities of S. lomentaria. Areas represented were usually poorly drained. Proper draining of these surfaces might increase the yield of harvestable P. columbina considerably. Proper drainage could be achieved by cutting channels in the rocks or by filling depressed areas with a sloping concrete surface. Happily, neither of these methods would seem to be practical.

Experiments at Avoca Point indicate that a large quantity

of P. columbina is destroyed at the settling stage by the action of molluscan grazers. Many slopes that could support heavy growths of P. columbina are kept bare of macroscopic plant life by gastropod grazing. The clearing experiment at Avoca Point indicates that the harvest of P. columbina could be greatly increased by temporarily clearing of the heavy grazers during the settlement time. The long term effect on the balance between plant life and the grazers would be hard to predict although the total number of surfaces that could be profitably treated would not represent a very great proportion of the total area occupied by these species of grazers on the peninsula.

Because of the large number of Porphyra-bearing rocks that are quite inaccessible, and the large quantities of P. columbina that are otherwise unsuited to harvesting, it is felt that harvesting the remainder would not jeopardize the alternate generation. Unharvested plants would produce enough spores to maintain the "Conchocoelis" stage population upon which the future harvests would depend.

The next step in determining the feasibility of harvesting this standing crop would be a commercial analysis of labor costs, production costs, and marketing prices. Such a commercial enterprise would certainly have a detrimental effect upon the educational value of the Kaikoura Peninsula, in terms of the future research programs of the Edward Percival Marine Laboratory.